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Effects of Post-Dam Flooding on Riparian
Substrates, Vegetation, and Invertebrate
Populations in the Colorado River
Corridor in Grand Canyon, Arizona

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EFFECTS OF POST-DAM FLOODING ON RIPARIAN SUBSTRATES,
VEGETATION, AND INVERTEBRATE POPULATIONS
IN THE COLORADO RIVER CORRIDOR IN GRAND CANYON, ARIZONA

Terrestrial Biology of the
Glen Canyon Environmental Studies

By

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Glen Canyon Environmental Studies

15 April, 1986

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ABSTRACT

Recent flooding exerted significant impacts on riparian substrates, riparian plant communities, and invertebrate herbivore populations in the Colorado River riparian corridor in Grand Canyon. Riparian substrates were scoured and leached by flooding in 1983. Base cation concentrations, %organic matter, and %silt+clay decreased relative to the substrate surface level following flooding, while pH remained unchanged. Increased %sand in this system implies increased rates of erosion, leaching, and desiccation of beach substrates, conditions which represent a significant decline in habitat quality for existing and future riparian plant life.

Flood-induced plant mortality was significant in this system, and reduced riparian plant abundance by more than 50% below the $1,700\text{m}^3/\text{sec}$ stage. Sources of mortality included 1) removal, which was dependent on plant architecture; 2) drowning/thrashing; and 3) burial beneath newly deposited fluvial sediments. Mortality was strongly differential, with relatively high survivorship of Tamarix chinensis, Salix exigua, and S. gooddingii, and low survivorship of Baccharis spp., Brickellia longifolia, and xeric-adapted species. Flooding did not eliminate any species from this system. In 1983 and 1984 flooding promoted germination of riparian plant seedlings, especially Tamarix and Baccharis; however, recovery of the habitat through recruitment of riparian plants is uncertain.

Flooding negatively affected invertebrate herbivore populations on Tamarix and Salix exigua in 1983, but was correlated with an outbreak of Opsius stactogalus (Homoptera: Cicadellidae) on Tamarix in 1984. Flooding also negatively affected terrestrial and fossorial invertebrate populations. Trophic relationships between terrestrial and aquatic components of the riparian ecosystem are complex in this system and are described in relation to suggested changes in the operating criteria of Glen Canyon Dam.

ACKNOWLEDGEMENTS

We wish to express our gratitude to all the fine scientists and assistants that accompanied us on these research ventures, especially Lorry Levine, Larry Rayburn, and Aubry Neas. Dr. Graydon Bell provided welcome assistance in statistics, and deserves the warmest thanks. Dr. Richard Foust and Mr. Tom Huntsberger of the Bilby Research Center at Northern Arizona University provided a great deal of much appreciated help in laboratory soil analyses. Dr. Raymond Turner kindly permitted us to examine his collection of Grand Canyon photographs. We received excellent advice and assistance from Dr. R. Roy Johnson, Dr. Steven W. Carothers, John Thomas, and other members of the National Park Service staff. Special thanks and admiration go to David Wegner, without whom this study would not have been possible.

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CHAPTER I: A GENERAL INTRODUCTION TO THE STUDY

The effects of regulated flow on terrestrial riparian soils, vegetation, and animal life are significant and complex, yet have received little attention from pedologists, ecologists, and habitat managers. The lack of research in this field is unfortunate given the general wildlife and recreational value of the riparian ecosystems which develop downstream from dams. Here in the arid Southwest, riparian lands are among the most ecologically productive terrestrial habitats, supporting a great diversity of plant life (Phillips in press), invertebrate life (Stevens 1976a, b) and vertebrate life, especially reptiles, birds and small mammals (Johnson and Carothers 1982; Johnson et al. 1985; and others). In the following study, we document changes in physical and chemical substrate characteristics, riparian plant populations, and riparian invertebrate populations that took place as a consequence of flooding in 1983, 1984, and 1985 in the post-dam Colorado River riparian corridor in Grand Canyon, Arizona.

Prior to the completion of Glen Canyon Dam in 1963, the Colorado River in Grand Canyon was subject to extreme variation in flow over the course of a year (Howard and Dolan 1981). Scouring spring floods removed virtually all perennial vegetation from the river banks and deposited vast quantities of fine sand, silt and clays. Flood-borne sediments kept the river water turbid and probably prevented algae (Cladophora) from colonizing the river bottom. The last pre-dam, ten-year flooding event of $3,530\text{m}^3/\text{sec}$ took place in 1957. Other record pre-dam flows include a $6,230\text{m}^3/\text{sec}$ flow in 1922 and a $8,500\text{m}^3/\text{sec}$ flow in about 1884 (R. Webb pers. comm.).

With the construction of the dam, the river's flow regime was dramatically altered (Howard and Dolan 1981) and the riparian zone became available to colonizing plants (Turner and Karpiscak 1980). The most vigorous invader species was exotic Tamarix chinensis, but native species also began to colonize this system about 1970 (Martin unpublished 1970). From 1963 to 1980, as the reservoir was filling, a dense zone of riparian vegetation grew up in the newly stabilized environment. Because flows were typically maintained below $820\text{m}^3/\text{sec}$, vegetation grew down to that stage, with stem density highest near this new high water line (Carothers et al. 1979). Riparian vegetation occurred in bands parallel to the river, with a pre-dam line of Fallugia paradoxa, Prosopis glandulosa and Acacia greggii. The new riparian zone vegetation consisted primarily of Tamarix, Salix exigua, several species of Baccharis, and Tessaria sericea, and occupied a dense zone at the water's edge. Invertebrate and vertebrate life gradually increased in diversity and reached high levels in the new riparian zone (Carothers and Aitchison 1976). Flooding was rare during this phase of the system's development. The largest post-dam flood, $1,576\text{m}^3/\text{sec}$, occurred in 1965, and regulated flows rarely exceeded $850\text{m}^3/\text{sec}$.

In 1980, a wet winter year, the reservoir finally filled and a flow of $1,400\text{m}^3/\text{sec}$ passed through the river corridor (Figure 1.0). This flooding event inundated much of the newly established vegetation and eroded a considerable portion of beach habitat. This flow was of

relatively short duration and resulted in little mortality among the riparian plant life. Above normal winter snowfalls in the spring of 1983 forced the Bureau of Reclamation to release a record post-dam discharge of $2,620\text{m}^3/\text{sec}$ through Grand Canyon, and that flood is of particular interest in this study. In 1984, and again in 1985, summertime flows were maintained at or above $1,130\text{m}^3/\text{sec}$ for prolonged periods of time, and this flooding continued to affect edaphic processes, riparian vegetation, and terrestrial animal life in this system (Figure 1.1).

Objectives of the Study

As part of the cooperative National Park Service and Bureau of Reclamation environmental assessment of the operating criteria of Glen Canyon Dam, the study reported here was designed to address the issue of how recent flooding and the operation of Glen Canyon Dam affected terrestrial riparian edaphic characteristics, vegetation, and invertebrate populations associated with riparian vegetation. Except for erosion, which is being studied by another research team in this environmental assessment, minor daily fluctuations in discharge levels do not appear to greatly affect terrestrial riparian substrates or vegetation and low-magnitude daily discharge fluctuations have not been examined in this study. Rather, it is prolonged discharge in excess of $850\text{m}^3/\text{sec}$ that exerts the most significant effects on this riparian system, and we have concentrated our studies on these recent, above-normal flows. Where possible, we will address management considerations relevant to circadian fluctuating flows.

In the following report we examine the effects of prolonged flooding in 1983, 1984 and 1985 on: 1) chemical and physical characteristics of terrestrial riparian substrates, 2) riparian vegetation, and 3) riparian invertebrate populations associated with that vegetation. Whether from the standpoint of soils or herbivores, we are primarily concerned with the ways in which flooding affects the producer trophic level in this ecosystem, riparian plant establishment, growth, and plant population dynamics.

Time Budget of Work Accomplished

A total of approximately 1,620 hours was spent directly on the research described in this report. The time devoted to each of the three aspects of this study was divided as follows:

Edaphic Research:

Field time, 100 hours (excluding travel time).

Laboratory time, 300 hours. Analysis and report preparation time, 240 hours.

Vegetation Research:

Field time, 300 hours (excluding travel time).

Laboratory time, 100 hours.

Data analysis and report preparation time, 180 hours.

Invertebrate Population Research:

Field time, 50 hours (excluding travel time).

Laboratory time, 160 hours.

Analysis and report preparation time, 120 hours.

NPS/BOR meetings and consultation, 80 hours.

Volunteer Time

Field and laboratory time in 1984 and 1985, 1,000 hours.

Field research was conducted from: three 17-18 day river research trips (June and August, 1984; June, 1985), of which two were funded and the latter was partially funded, with 5 to 6 volunteers/trip; one 3-day kayak trip through Marble Canyon in October, 1984; one 4-day raft trip from Havasu Creek to Diamond Creek in mid-November, 1985; four commercial river trips; and several land-based trips to Lees Ferry and the Mile 43 vicinity. Travel time on these expeditions was not included in the above summary of research time for this study.

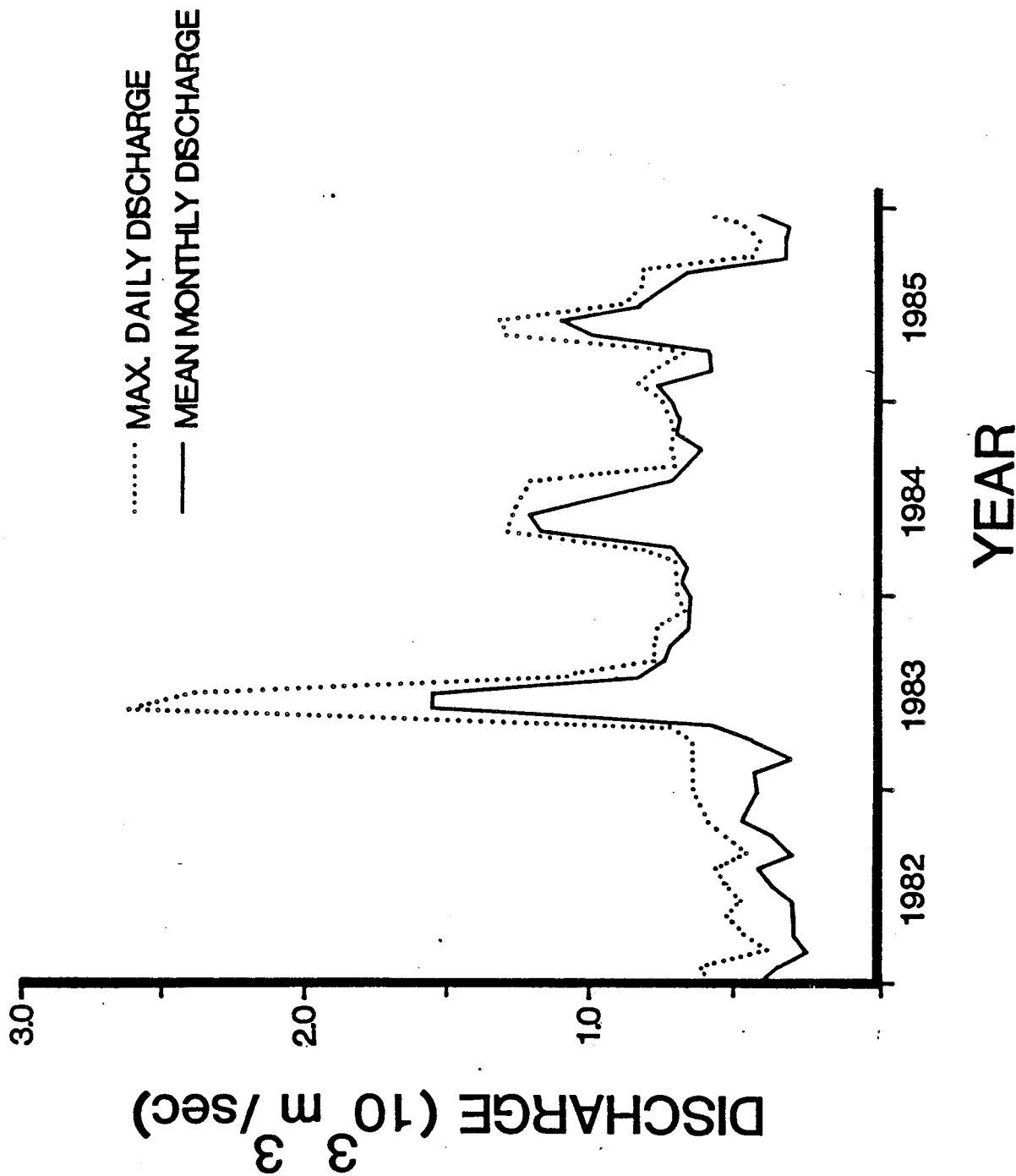


FIGURE 1.0: MAXIMUM DAILY DISCHARGE AND MEAN MONTHLY DISCHARGE FROM GLEN CANYON DAM, 1982-1985, MEASURED AT THE U.S. GEOLOGICAL SURVEY GAUGING STATION AT LEES FERRY, ARIZONA.

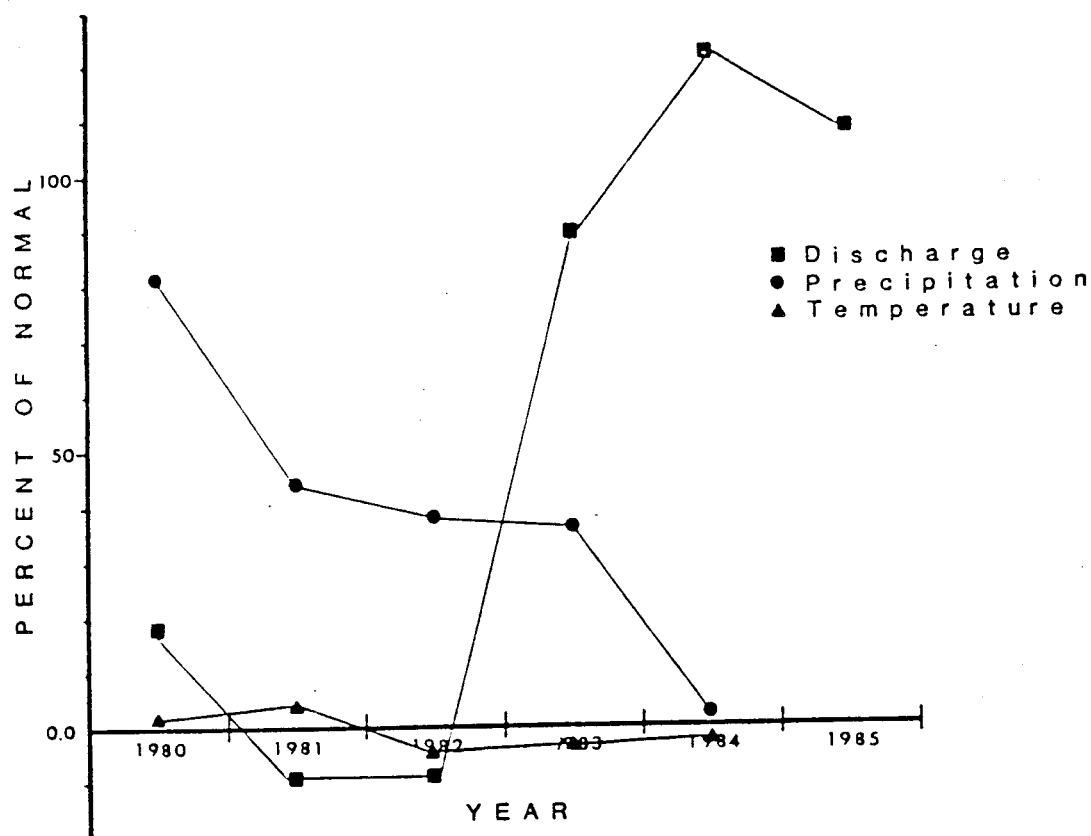


FIGURE 1.1: PERCENT OF NORMAL MEAN ANNUAL DISCHARGE FROM GLEN CANYON DAM, TOTAL ANNUAL PRECIPITATION, AND MEAN ANNUAL TEMPERATURE IN GRAND CANYON FROM 1980 TO 1985. DISCHARGE DATA FROM LEES FERRY, WITH A NORMAL POST-DAM DISCHARGE OF $360\text{m}^3/\text{sec}$. (HOWARD AND DOLAN, 1980). CLIMATIC DATA TAKEN FROM SELLERS AND HILL (1974) AND ANNUAL N.O.A.A. REPORTS (1980-1985) FOR PHANTOM RANCH.

CHAPTER II: THE EFFECTS OF FLOODING ON RIPARIAN SUBSTRATES

Introduction

Riparian substrates in arid regions are typically of fluvial origin, and often occur as well-stratified, superimposed laminae of clays, silts and/or sands. Because of regular disturbance and inundation of these relatively unweathered fluvial entisols, inceptisols and mollisols (U.S. Soil Conservation Service 1975) may be considered as torrifluvents or, on more stable sites with increased organic matter, as haplustolls (Brock 1985). Many authors do not consider fluvial deposits as "soils" in the pedological sense of the word (e.g. Galel' and Malan'in 1977) because of the unweathered state of such substrates.

Fluvial substrates in Grand Canyon occur in pre- and post-dam terraces and have not been described in detail (Carothers et al. 1979; Howard and Dolan 1981; Scala unpublished 1984). Riparian substrate characteristics in the Colorado River corridor have been examined in two unpublished studies. In a preliminary survey of soil-plant relationships, Harrison (unpublished 1981) examined pH, organic matter, nitrate, phosphate, and texture on a small number of samples from near-river, mid-beach, and pre-dam terraces. He found the mid-beach zone (corresponding to our Zones B and C, see below) characterized by 1) a lack of vegetation, 2) low nitrogen status, and 3) larger particle size substrates sorted by eolian processes. Harrison suggested that vegetation density increased on sites with relatively small particle size, low sand content, and high nitrate concentration. Unfortunately, no details of collection sites, methodology, or statistics were provided in his report.

Scala (unpublished 1984) examined relationships between riparian vegetation, river hydrology and sedimentation in the post-dam system prior to 1983. Using principal components analysis he found base cation concentration to be negatively correlated with particle size. He also found that tributaries exerted a strong local influence on substrate texture. Scala described preferences of vegetation for certain substrate characteristics; for example, he found Tamarix associated with finer sediments than either Salix or Tessaria. All base cation species except potassium showed a pronounced "bulge" at 50cm depth. Potassium was highest at the surface beneath mesquite and was also found in significant concentrations beneath Tamarix and Tessaria. Potassium concentration declined with depth. In an analysis of site-averaged substrate characteristics in riverside, intermediate, and pre-dam terraces, Scala found lower values of percent silt and base cations among riverside sites than among pre-dam sites. Percent sand was greater at all depths on riverside sites than on pre-dam sites.

Scala (op. cit.) also described base cation concentration in post-dam river water and compared it to that in riparian substrates. The post-dam river carried a dissolved load comprised of 40.1% Ca^{2+} , 43.0% Na^{+} , 14.8% Mg^{2+} , and 0.2% K^{+} :

$$\text{Na} = \text{Ca} > \text{Mg} \gg \text{K}$$

In contrast the riparian substrate exhibited Ca^{2+} concentrations commonly 10 to 30 times greater than Na^+ or Mg^{2+} and K^+ 3 to 10 times lower than Na^+ or Mg^{2+} :

$$\text{Ca} \gg \text{Na} = \text{Mg} > \text{K}$$

Scala attributed cation concentration differences between the river and riparian substrates to eolian and colluvial transport of dust and debris in the terrestrial substrates.

Recent beach sand studies have been undertaken by Beuss (unpublished and pers. comm.) in this system. Seiving analysis was conducted on samples from approximately 30 beaches throughout Grand Canyon. Preliminary analysis of his data show no change in the %sand following recent flooding in this system; however, his analyses are still underway. He sampled surface sediments on beaches with relatively high levels of recreational impact.

Objectives

These studies left important questions unanswered, such as the general course of pedogenesis in this system, the effects of streamflow regulation on substrate characteristics, and the nature of interactions between vegetation and substrate. These questions, as well as those related to the effects of recent, high amplitude flooding events on riparian vegetation stimulated the present study. Therefore, we undertook a research plan designed to address the following questions regarding the effects of flooding on physical and chemical substrate characteristics from the standpoint of their impact on riparian vegetation in this system:

- 1) How did flooding in 1983-1984 affect substrate pH, cation concentrations, texture, and organic content, relative to the exposed substrate surface available to vegetation?
- 2) What are the consequences of these flood-induced substrate changes on subsequent growing conditions for riparian plants?
- 3) What general pedogenic trends in substrate characteristics have taken place through time in the post-dam era?
- 4) Under what operating criteria can Glen Canyon Dam maximize the beneficial effects of flow regulation for terrestrial substrate quality in this system?

Methods

Efforts were undertaken to describe riparian substrates and examine the effects of discharge stage, reach type, distance from Glen Canyon Dam, and vegetation cover on substrate characteristics. Twenty of Scala's (op. cit.) sample sites were visited and resampled in the summer and fall of 1984 (Figure 2.1). Scala sampled these sites with Stevens in

1981 and the sites we selected to resample were those that best represented characteristic floodzones, terraces, cover types, and substrates. Sites were chosen to minimize disturbance from tributaries and human (recreational) impacts. By carefully selecting our sites we were able to determine how recent flooding events in this system influenced edaphic parameters important to riparian vegetation. These twenty sites were located in four of the Bureau of Reclamation's five reaches in Grand Canyon, from Lees Ferry to Mile 198.5R.

In re-sampling the 1981 sites we attempted to determine how substrate conditions had changed for existing and potential riparian plant life at each site. We resampled at the same location but collected our samples using the surface as our baseline. In several cases the substrate surface had been so completely altered that precise relocation of the original site was not possible. For example, sites at Miles 41.0R and 50.5L were thoroughly scoured in 1983 and are presently exposed only at flows below approximately $500\text{m}^3/\text{sec}$. Prior to 1983 the surface of these sites lay at approximately the $1,000\text{m}^3/\text{sec}$ level and was covered by extensive stands of Salix exigua. Resampling at these sites was conducted at approximately the same relative surface location. Where precise relocation of the site was not possible, only the data from homogeneous, extremely uniform sites were used (e.g. in open beach substrates).

At each site a 1.5m hole was excavated with a shovel and 500g samples were extracted at depths of 5, 35, 50, 75, 100, and 150cm (where possible), relative to the surface. Samples were extracted from the exposure with a plastic scoop or plastic bag to prevent contamination. Samples were placed in labeled plastic bags and the following information was recorded: location, date of collection, detailed observations on the substrate profile, condition of the site, approximate stage of the surface, and changes in vegetational cover type engendered by flooding. These parameters were considered to influence substrate chemistry and structure. Samples were returned to the laboratory where they were air-dried at 20°C prior to analysis.

Floodzones were defined as follows: Zone A extended from the $700\text{m}^3/\text{sec}$ stage to $1,130\text{m}^3/\text{sec}$ and was the zone of greatest flooding impact; Zone B lay between $1,130\text{m}^3/\text{sec}$ and $1,700\text{m}^3/\text{sec}$ and sustained less prolonged inundation in 1983; Zone C lay between $1,700\text{m}^3/\text{sec}$ and $2,500\text{m}^3/\text{sec}$ at the top of the 1983 floodzone; and Zone D lay above the $2,500\text{m}^3/\text{sec}$ stage--above the zone of impact from the 1983 flooding event. The approximate stage of a sample site was determined in relation to known stage lines and the top of the 1983 flood zone. Relatively constant discharge during the first half of 1984 left a distinct "bathtub ring" along the river bank at approximately the $1,200\text{m}^3/\text{sec}$ level, which served as a useful reference during our sampling.

Cover type categories included 1) sites that had been open beach sites in 1981 (all remained open beach sites in 1984); 2) sites which had been covered by S. exigua in 1981; 3) Tamarix chinensis sites; and 4) Zone D sites with miscellaneous vegetational cover (Prosopis, Acacia, Larrea, Tamarix, and grasses).

For 17 of the 20 sites, we obtained Scala's (op. cit.) original 1981 35cm-depth samples, which we had compared with our surface-relative 1984 sampling program. Scala's samples were subjected to the same analyses as our 1984 samples, allowing us to make accurate comparisons of substrate changes before and after the flooding.

In the laboratory the following analyses were performed: pH, texture (%sand, %silt+clay, and %clay) and selected cation concentrations. In addition, percent burnable organic content plus carbonates was determined for samples at 35cm depth for which matching samples from the 1981 survey were available.

Colorimetric determination of sample pH was made using a Morgan soil pH kit. Several grams of sediment were placed in a sampling dish and saturated with a pH sensitive dye. After 3 minutes the color of the sample was matched against standard soil pH color charts. Colorimetric determinations were compared with those made using an electronic Photovolt pH meter and were found to be generally comparable. To accurately determine pre- to post-flooding changes, pH was determined by electronic probe for the matched 1981-1984 35-cm depth.

The concentrations of sodium (Na^+), potassium (K^+), calcium (Ca^{2+}) and magnesium (Mg^{2+}) cations were determined in all samples. Cation extraction was performed using a weak acid and was performed in accordance with standard soil chemical techniques (Folk 1980). All glassware was acid-washed prior to use to prevent contamination. A subsample of each sample was dried at 40°C to constant weight; 12.5g of dried substrate was placed in 50ml of a weak acid solution ($0.05\text{ N HCl} + 0.025\text{ N H}_2\text{SO}_4$) and shaken on a mechanical shaker for 5 minutes. This solution was immediately filtered by suction twice to remove all suspended particles, placed in a labeled, plastic bottle, and refrigerated. By using a weak acid extraction solution and a short extraction time we approximated levels of cations available to plants (Scala op. cit.) To ensure precision, the acid equivalence of the extraction solution was verified against a known concentration of NaOH. The acid equivalence proved to be 0.077 N acid, extremely close to the 0.075 N required by the extraction protocol.

Cation concentrations were determined under standard conditions and procedures using a Perkin-Elmer 560 Atomic Absorption Spectrophotometer (Perkin Elmer 1982). Sample solutions were diluted according to cation concentrations: for analyses of Na^+ and K^+ , samples were diluted 1:8.5 the Mg^{2+} dilution factor was 1:45; and that for Ca^{2+} was 1:455.6. Samples were diluted with 10,000ppm CsCl and 10,000ppm La solutions to prevent phosphorus binding. Diluted solutions were vortexed for 5 seconds and concentrations were determined at the appropriate transmission wave length for each cation against EPA standard solutions of each cation.

Aspects of substrate texture were determined using two techniques. First, we matched Scala's use of the Bouyoucos (1927) particle size determinations. Fifty g of dried sample were placed in a 1 N calgon (TM) solution and slaked for 15 minutes. This solution was vigorously mixed in a commercial milkshake blender for 15 minutes. The solution

was then placed in a 2-liter glass Bouyoucos cylinder and promptly shaken for 20 seconds. A soil hydrometer was immediately placed in the cylinder and readings were made at 40 seconds (the standard length of time for sand-sized particles to drop out of solution) and again at 2 hours (the time required for silt-sized particles to drop out of solution). Temperature was recorded at both readings and used to correct %sand and %silt values. This technique is of marginal value for %sand analyses because of the difficulties with obtaining accurate readings in such a short period of time, and %sand data were not regarded as reliable. Consequently, only %clay data are included in our results.

Sieving analysis, a more accurate analytical technique, was used to determine %sand and %silt+clay in the samples. Samples were air dried and mechanically shaken through a stack of sieves with known, progressively smaller, diameters. The weight of the contents of each sieve was determined in relation to the total weight of the sample. The U.S. Geological Survey staff in Tucson graciously performed these time-consuming sieving analyses for all samples. The U.S. Geological Survey defines sand-sized particles as being between 0.0625mm and 1.000mm, and silt or clay particles as less than 0.0625mm (J.Graf pers. comm. 1985).

Organic content of the matched 35cm depth samples was determined by drying subsamples at 100°C to constant weight, weighing the dried sample, ashing it at 500°C to constant weight, and then reweighing it. While extremely simple, this procedure burns carbonates along with the organic matter; however, according to Beuss (pers. comm.) fluvial sediments in this system consist almost entirely of quartz (SiO_2). Burning therefore provides a relatively accurate index of organic content.

Data were analyzed using SPSS (Nie et al. 1975) and Minitab (Ryan et al. 1976) statistical packages. Textural and %organic content analyses were percentage data by volume, not count data, and therefore a search was made for the best data transformation technique to stabilize the variance. \log_{10} , square root, arcsin, and squaring transformations were tried; however, raw percentage data provided the best fit of all techniques tried in regression analyses.

Results

In general the substrates of the Colorado River riparian corridor were found to consist of unweathered, alluvial, light-colored, fine silty sands or sandy silts with little organic matter. In pre-dam terraces, where the sediment profile remained undisturbed by flooding, these sediments were deposited as stratified, superimposed laminae of texturally uniform, hydrophobic silt loam, loam, sandy loam, loamy sand or sand (as defined by Bodman and Mahmud 1932). In contrast, the sediments in zones A and B were typically sand or loamy sand, more coarse in texture, less stratified, and non-hydrophobic. Buried, inundated pre-dam sediments in Zone A were often odoriferous and gleyed (bluish in color), indicating the development of reduction environments during inundation (Birkeland 1984).

All of the sites in Zones A and B that were resampled in 1984 had been altered by recent flooding. All 4 open beach sites in 1981 remained as open beach sites. Four of 5 sites covered with Salix exigua in 1981 were entirely devoid of vegetation in 1984. Of the 5 sites covered by Tamarix in zones A and B, 1 had been devegetated, 3 sustained significant reduction in cover, and 1 site was relatively undamaged. Thus, only 1 of 10 vegetated sites was relatively unaffected by flooding, while 30% sustained significant damage and 60% were completely devegetated.

Flood-induced substrate disturbance in this system was not merely surficial. The absence of stratification, structure, and roots in Zone A and B sample pits indicated that a significant amount of scouring, burial and redeposition occurred during flooding. Three of 14 sites (21.4%) in zones A and B had been scoured, 5 of 14 sites (35.7%) received new deposits of fluvial sediments, and 6 of 14 sites (42.9%) were relatively unchanged. At the Mile 43.1R site, sediments were removed to a depth of at least two meters as the stage increased to 1,700m³/sec in 1983. Scouring occurred at Mile 165.0R and at all sites occupied by Salix exigua except those at Mile 1.2R and 50.2R. Following subsidence of the 1983 floodwaters, many beaches reappeared with almost precisely the pre-1983 morphology and surface elevation; however, sampling these new beach deposits after subsidence of floodwaters revealed little laminar stratification and no roots to 1.5m depth. These observations as well as physical and chemical analyses of sediments suggest that eddy beach deposits were replaced as a consequence of flooding, with scouring possibly occurring during rising discharge, particularly above the 1,130m³/sec stage, and redeposition during subsidence of floodwaters.

Substrate pH

Differences in substrate pH were determined between vegetation cover types, between discharge zones (floodzones), and before and after the 1983 flooding event at relative substrate surfaces. Colorimetric analyses showed that substrate pH in 1984 varied slightly between cover types and between inundated and non-inundated zones (Table 2.1, Figure 2.2). The mean 1984 depth-averaged (DA) pH for all 20 sites was 8.17; however, DA pH values were lowest in Zone D (mean = 8.03, n=6), with progressively higher values in Tamarix stands (8.13, n=7), former Salix exigua stands and open beaches (8.24, n = 5 for both). DA pH values between the 4 cover types were marginally significantly different (p=0.051, df=3,16), with Zone A Tamarix sites intermediate between Zone D and non-Tamarix Zone A sites (Table 2.2). DA pH values in Zone A Tamarix sites were not significantly different from Tamarix sites in Zone D (p=0.876, df=1,5). Zone A DA pH values averaged 8.27, while the mean in Zone D was significantly lower at 8.08 (p=0.025, df=1,18).

Electronic probe analyses of 35cm depth pH changes between 1981 and 1984 relative to substrate surface level, indicated that flooding homogenized differences in substrate pH which existed between the four cover types prior to 1983 (Table 2.3, Figure 2.2). Prior to flooding the mean pH values for inundated Tamarix sites at 35cm depth was 7.75 (n=4), while mean values for Salix exigua (8.03, n=5) and open beach sites (8.15,

n=4) were significantly higher ($p=0.040$, $df=1,4$). In 1984 differences between these cover types in Zone A were non-significant at 35cm depth. The Paria Beach site at Mile 1.2R was excluded from these and other substrate comparisons because of its proximity to a major tributary.

Regression of substrate pH at 35cm depth on all beaches (except Paria Beach) in Zone A against distance downstream showed no correlation and was nonsignificant in 1981 (R^2 approaching 0.0; Table 2.5). In 1984 correlation between these factors remained non-significant, but R^2 increased to 0.131 ($n=1,7$). Regression of DA pH values with distance downstream from Glen Canyon Dam for unvegetated Zone A beach sites showed no correlation ($R^2=0.0\%$ adjusted for df ; $p=0.231$, $df=1,7$), as indicated in Table 2.4.

Trends in pH with depth were comparable but not significantly different between Zone A and Zone D sites in the upper 100cm of the profiles; however, some divergence in pH was noted at 150cm depth, where the pH of non-inundated sites declined while that of the inundated sites increased (Figure 2.4). No correlation was found (R^2 approaching 0.0) between pH and substrate depth.

Regression of pH at 35cm depth with stage (location of sampling pit relative to the river) showed these two variables to be weakly negatively but not significantly correlated in 1981 ($R^2 = 0.129$; $p<0.10$, $df = 1,15$), a relationship which remained unchanged in 1984 ($R^2 = 0.115$; $p<0.10$, $df = 1,18$) (Table 2.6).

Base Cations: Sodium Cation Concentrations

In 1984 sodium (Na^+) concentrations averaged 101.2ug/g for all 20 sites, with lowest values in former *S. exigua* stands (20.7ug/g, $n=5$), slightly higher values in Zone A *Tamarix* stands (49.6ug/g, $n=4$) and open beach sites (51.9ug/g, $n=5$), and much higher in all Zone D sites (243.8ug/g, $n=6$); however, cover type differences were not significantly different ($p=0.193$, $df=3,16$) because *Tamarix* occupied both inundated and non-inundated zones (Tables 2.1 and 2.2). DA sodium concentrations in Zone A *Tamarix* sites averaged 49.6ug/g ($n=4$), while those in Zone D averaged 405.7ug/g ($n=3$), significantly different at $p=0.027$ ($df=1,5$). Overall DA sodium concentrations averaged 40.1ug/g in Zone A and 243.8ug/g in Zone D, a difference that was significant at $p=0.004$ ($df=1,18$).

Analyses of between-year differences in sodium concentrations at 35cm depth show a decline in Na^+ concentration in all cover types through time relative to substrate surface level (Table 2.3, Figure 2.3). In all Zone A sites this decline was significant, from a mean of 51.8ug/g in 1981 to 22.0ug/g in 1984 ($p=0.018$, $n=12$); however, Na^+ concentrations did not change significantly over this interval in Zone D ($p=0.625$, $df=3$).

Regression of DA sodium concentrations on unvegetated beach sites in 1984 with distance downstream from the dam revealed no significant correlation ($R^2=0.0$ adjusted for df ; nsd , $df=1,7$), as shown in Table 2.4. Likewise, regression of Na^+ concentration at 35cm depth on Zone A and B beaches with distance from Glen Canyon Dam in 1981 and 1984

and B beaches with distance from Glen Canyon Dam in 1981 and 1984 indicated no correlation between these variables (Table 2.5).

Sodium concentrations in 1984 in Zone D showed a distinct "bulge" at 50cm depth (Figure 2.5). Zone A sample pits revealed a similar bulge at 100cm depth, indicating that sodium was being leached down through the profile. Sodium is highly soluble and it was probably lost through leaching in this system, rather than being drawn to the surface by capillary action (Birkeland 1984).

Regression of sodium concentration at 35cm depth as a function of stage produced a significant, positive correlation in 1981 ($R^2 = 0.266$; $p < 0.025$, $df = 1,15$) and an improved correlation in 1984 ($R^2 = 0.378$; $p < 0.001$, $df = 1,18$), as shown in Table 2.5. This further suggests that sodium is being leached from the system by flooding.

Base Cations: Potassium Cation Concentrations

Potassium (K^+) concentrations, like sodium, were low in this system, with an overall DA mean of 51.5ug/g ($n=20$), as shown in Table 2.1. The lowest values were obtained in Zone A in former S. exigua stands (mean=14.9ug/g, $n=5$), with slightly higher values on open beaches (23.8ug/g, $n=5$) and Tamarix sites (42.5ug/g, $n=4$), and much higher values on Zone D sites (111.0ug/g, $n=6$). Table 2.2 shows that differences between cover types for this cation were significant at $p < 0.001$ ($df=3,16$). The S. exigua and open beach sites were significantly lower in DA K^+ concentrations than were Zone A Tamarix, which were significantly lower than Zone D values (Table 2.1). DA Zone A Tamarix sites had significantly lower K^+ concentrations than did Zone D Tamarix sites (mean=93.6ug/g $n=3$). Overall differences between Zone A and Zone D K^+ concentrations were significant at $p < 0.001$, $df=1,18$.

Potassium cation concentrations at 35cm depth declined from a mean of 34.8ug/g to 17.0ug/g on Zone A sites between 1981 and 1984 ($p < 0.001$, $n=13$; Table 2.3), relative to substrate surface level. In contrast, the non-inundated Zone D sites showed no significant decline in K^+ concentration.

Table 2.4 shows that DA K^+ concentration on unvegetated 1984 beaches was not correlated with distance from Glen Canyon Dam ($R^2=2.5\%$ adjusted for df ; $p > 0.05$, $df=1,7$; Table 2.4), despite a relatively strong positive correlation between 35cm depth concentrations and distance (Table 2.5). This discrepancy was attributed to high K^+ concentrations at the surface (especially beneath Prosopis and Tamarix canopies), with consistent depletion through depth in the profile (Figure 2.5).

Potassium concentrations were markedly higher at the surface on Zone D sites, with a slight bulge at 75cm depth. K^+ concentrations were uniformly minimal throughout the Zone A profiles (Figure 2.5). The trend Scala (op. cit.) reported of high K^+ concentrations at the surface beneath Tamarix was found only on non-inundated Zone D sites (Figure 2.3). Zone A potassium concentrations were uniformly low throughout the profiles. Leaching is the most likely cause for the disappearance of high surface K^+ concentrations.

Regression of potassium concentrations at 35cm depth against stage showed a positive, statistically significant relationship in 1981 ($R^2 = 0.478$; $p < 0.005$, $df = 1,15$) and a stronger, more significant correlation in 1984 ($R^2 = 0.604$; $p < 0.001$, $df = 1,18$), as indicated in Tables 2.3 and 2.6.

Base Cations: Calcium Cation Concentrations

Calcium (Ca^{2+}) concentrations were much higher than Na^+ or K^+ concentrations in this system, with an overall 1984 mean for all 20 sites of 1,406.3ug/g (Table 2.1). DA Ca values were lowest on former S. exigua sites (mean=1,200.4ug/g, $n=5$), slightly higher on open beach sites (1,300.2ug/g, $n=5$), still higher on Zone A Tamarix sites (1,497.0ug/g, $n=4$), and higher still on Zone D sites (1,607.7ug/g, $n=6$). Differences between these cover types were significant at $p=0.001$ ($df=3,16$), with willow and open beach sites significantly lower than Zone A Tamarix and all Zone D sites (Table 2.2). Analysis of DA Ca^{2+} concentrations in Zone A versus Zone D Tamarix stands showed no significant differences ($p=0.312$, $df=1,5$). Overall, Ca^{2+} concentrations were significantly higher on Zone D sites as compared to Zone A sites ($p=0.002$, $df=1,18$; Table 2.2).

Calcium concentrations at 35cm depth declined significantly from 1981 to 1984 on inundated sites, relative to substrate surface level ($p=0.042$, $df=12$); however, inundated Tamarix sites showed no significant decline between years (Table 2.3, Figure 2.3). Zone D sites showed no significant change in Ca^{2+} concentrations between years.

Table 2.4 shows that DA Ca^{2+} concentrations on Zone A and B beaches were strongly correlated with distance downstream from Glen Canyon Dam in 1984 ($R^2 = 0.478$; $p < 0.05$, $df = 1,7$), although regression of Ca^{2+} concentration at 35cm depth on Zone A and B beaches showed no correlation with distance downstream from Glen Canyon Dam in 1981 or 1984 (Table 2.5). Lack of correlation may be attributable to tributary input of Ca^{2+} in this system.

A regression of Ca^{2+} concentration against depth was not significant; however, Ca^{2+} concentration reached a peak at the surface and at 50cm depth in Zone D soils. The surface peak was mirrored in Zone A soils, but the subsurface peak declined to 100cm (Figure 2.5).

Regression of Ca^{2+} concentration at 35cm depth against stage was not significant in 1981; however, in 1984 a significant positive relationship was observed ($R^2=0.253$; $p < 0.025$, $df=1,18$; Table 2.6).

Base Cations: Magnesium Cation Concentrations

Overall DA magnesium (Mg^{2+}) concentrations averaged 235.9ug/g at 20 sites in 1984 (Table 2.1). The lowest DA Mg^{2+} concentrations were found on open beach (mean=185.6ug/g, $n=5$) and former S. exigua sites (195.3ug/g, $n=5$), suggesting that leaching removed Mg^{2+} from inundated substrates. Higher concentrations were found on Zone A Tamarix sites (251.9ug/g, $n=4$), and the highest values were recorded from Zone D sites (301.1ug/g, $n=6$). Differences between cover types were significant at $p=0.012$ ($df=3,16$), and Duncan's multiple range test revealed that open beach and S. exigua sites had significantly lower DA Mg^{2+} concentrations

than did Zone A Tamarix sites or Zone D sites (Table 2.2). Differences in DA Mg^{2+} concentrations between Zone A and Zone D Tamarix stands were not significantly different ($p=0.277$, $df=1,5$).

Comparison of 1981 to 1984 samples at 35cm depth showed that Mg^{2+} concentrations decreased slightly but non-significantly between years relative to substrate surface level (Table 2.3, Figure 2.3).

No significant correlation was found between DA Mg^{2+} concentrations and distance downstream from Glen Canyon Dam ($R^2=10.1\%$ adjusted for df ; nsd) in 1981 or 1984 at 35cm depth (Table 2.5), or in 1984 for DA values (Table 2.4).

Magnesium concentrations increased slightly with depth in Zone D, but not in Zone A (Figure 2.5). A slight bulge in Mg^{2+} concentration was observed at 75cm on Zone D sites, whereas a slight bulge was found at 100cm depth on Zone A sites.

Mg^{2+} concentrations at 35cm depth were not correlated with stage in 1981, but were weakly correlated with stage in 1984 ($R^2 = 0.332$; $p<0.005$, $df = 1,18$), as indicated in Table 2.6.

Total Base Cation Concentrations

The total mean DA base cation concentration, here considered as the sum of Na^+ , K^+ , Ca^{2+} , and Mg^{2+} concentrations, was 1,794.8ug/g for all 20 sites (Table 2.1). Table 2.2 shows that differences between cover types were significant at $p=0.002$ ($df=3,16$), with concentrations on former S. exigua sites (mean=1,431.2ug/g, $n=5$) and open beach sites (1,561.4ug/g, $n=5$) significantly lower than Zone A Tamarix sites (1,838.0ug/g, $n=4$), and highest values on Zone D sites (2,263.5ug/g, $n=6$). Zone A Tamarix sites had lower total cation concentrations than Zone D Tamarix sites at $p=0.032$ ($df=1,5$). Total cation concentrations among all Zone A sites were significantly lower than Zone D concentrations at $p<0.001$ ($df=1,18$).

Total cation concentrations at 35cm depth declined significantly relative to the substrate surface level from 1981 to 1984 among all Zone A and B cover types except Tamarix ($p=0.014$, $df=12$), but total cation concentrations were not significantly different between years in Zone D (Table 2.3).

While total cation concentrations at 35cm depth were not correlated with distance downstream in 1981 or 1984 (Table 2.5), DA total cation concentrations were strongly and positively correlated with distance ($R^2 = 0.455$; $p<0.05$, $df = 1,7$; Table 2.4).

Regression of total cations against depth showed no correlation between these factors; however, this was confounded by the non-linear distribution of cations in the profile. Depth profiles (Figure 2.5) showed highest total cation concentrations at 75cm depth in Zone D, whereas an analogous, less distinct bulge occurred at 100cm depth in Zone A profiles.

Regression of total cation concentrations at 35cm against stage was positive and significant in 1981 ($R^2 = 0.402$; $p < 0.005$, $df = 1,15$), and was stonger in 1984 ($R^2 = 0.515$; $p < 0.001$, $df = 1,18$). All of these observations indicate the removal of base cations (largely dominated by calcium in this system) from this system by flood-induced leaching.

Percent Organic Matter and Burnable Carbonates

Substrates with 0.2% to 10% carbon are considered as "mineral soils" (Allen 1974) and all samples collected fell into this range. The technique used to assess %organic matter was relatively crude, but it established a maximum possible value for organic material in the samples. The overall mean %organic matter+carbonates among all 20 sites at 35cm depth was 0.77% and varied between cover types and zones (Tables 2.1 and 2.2). Percent organic matter + carbonates was lowest in open beach and former S. exigua sites (mean=0.32% and 0.33%, respectively), slightly higher in Zone A Tamarix sites (0.49%), and more than 3-fold higher in Zone D sites (1.70%). Duncan's multiple range test showed Zone A Tamarix sites were intermediate between the beach sites and the Zone D sites, but Zone A Tamarix sites were not significantly different from Zone D Tamarix sites. Differences between the two zones were pronounced ($p < 0.001$, $df=1,18$). with Zone A sites (mean = 0.37%, $n = 14$) significantly lower than Zone D sites (1.70%; $p < 0.001$, $df = 1,18$).

The %organic+carbonate values at 35cm depth were significantly lower in 1984 than in 1981 across all sites, relative to substrate surface level ($p=0.027$, $df = 16$; Table 2.3, Figure 2.2). While 35cm depth values in 1984 were significantly lower than 1981 values in Zone A ($p=0.002$, $df=12$), between-year differences in Zone D were not statistically different ($p=0.919$, $df=3$).

Linear regression of Zone A and B beach %organic+carbonate values from 35cm depth in 1981 with distance downstream from Glen Canyon Dam revealed no significant relationship, but this same analysis on 1984 data provided a significant positive relationship against distance from the dam ($R^2 = 0.513$; $p < 0.05$, $df = 1,8$; Table 2.5).

Regression of %organic+carbonate at 35cm depth against stage was nonsignificant in 1981, but was strongly significant in 1984 ($R^2 = 0.565$; $p < 0.001$, $df = 1,18$; Table 2.6).

Substrate Texture: Percent Sand

Substrate samples from the Colorado River riparian corridor in Grand Canyon consisted of fluvial, typically fine, silty sand with minor to moderate amounts of clay.

The overall DA %sand in 20 substrate samples was 76.9% in 1984 (Table 2.1). Cover types were significantly different ($p = 0.001$, $df = 3,16$), with open beach and former S. exigua sites containing significantly higher DA proportion of sand-sized particles (means = 96.8% and 92.5%, respectively; $n = 5$) than Zone A Tamarix sites and Zone D sites (75.9% and 48.0%, respectively; $n = 4$ and 6, respectively; Table 2.2). The DA mean %sand on Zone A and B beach sites was 89.3% ($n = 14$), significantly higher than the Zone D DA mean of 48.0% ($p < 0.001$, $df=1,18$). Zone A Tamarix average DA mean was 75.9%, while Zone D Tamarix DA mean was

39.5% sand. The similarity between Zone A and Zone D Tamarix sites between years can be attributed to two factors: (1) the substrate beneath dense Tamarix stands was complex, consisting of numerous laminae of fine, erosionally resistant pre-dam sediments (Scala, op. cit.); and (2) dense root and above-ground vegetation protected the substrate by holding the soil and by ponding, reducing current velocity in densely vegetated sites and consequently reducing hydraulic erosion.

Analysis of 35cm depth data from 1981 and 1984 relative to substrate surface level showed that the %sand increased significantly in Zone A and B beach sites ($p = 0.039$, $df = 7$), and on former S. exigua sites, but rose non-significantly in Zone A Tamarix sites (Table 2.3, Figure 2.6). Retention of the substrate on Zone A Tamarix sites kept the increase in %sand in all Zone A and B sites statistically non-significant. The %sand on Zone D sites did not change significantly between 1981 and 1984.

Table 2.5 shows that the %sand in Zone A and B beaches at 35cm depth did not correlate with distance from Glen Canyon Dam in 1981; however, a significant negative correlation between these two variables was evident in 1984 ($R^2 = 0.378$; $p < 0.05$, $df = 1,7$). This trend was confirmed with the 1984 DA %sand in Zone A and B beaches, which produced a negative correlation with distance downstream from the dam ($R^2 = 0.434$; $p < 0.05$, $df = 1,7$; Table 2.4). These correlations may be attributed to erosion, redeposition, and/or tributary influences.

As noted above, fluvial sediments in this system consist of interbedded laminae of relatively uniform size particles, and thus particle size varies erratically through the profile. Analysis of texture by depth revealed uniformly %sand with little variation though the profile in Zone A. Significantly lower %sand and more variable textures were found in Zone D profiles (Figure 2.6). A weak, negative correlation between %sand at 35cm depth and stage in 1981 ($R^2 = 0.179$; $p < 0.10$, $df = 1,15$) was stronger following flooding in 1984 ($R^2 = 0.511$; $p < 0.001$, $df = 1,18$), indicating that fine particle sediments were entrained and transported out of the system by flooding (Table 2.6).

Substrate Texture: Percent Silt and Clay

Because large sands and gravel-sized ($>2\text{mm}$) particles are virtually non-existent in these fluvial deposits, the %silt+clay follows precisely the opposite trend as that observed for sand -- little silt and clay on Zone A beach sites in 1984, and significantly higher proportions of these finer particles in Zone D and Tamarix sites. The overall 1984 DA mean value for all 20 sites was 22.7% silt+clay (Table 2.1). One way analysis of variance showed that significant differences existed between cover types (Table 2.2), with former S. exigua (mean = 3.2%) and open beach sites (7.5%) having significantly lower %silt+clay than Zone A Tamarix sites (23.6%) or Zone D sites (51.0%) at $p = 0.002$ ($df = 3,16$). The %silt+clay was significantly lower on Zone A sites as compared to Zone D ($p = 0.001$, $df = 1,18$). Zone A Tamarix sites had a significantly lower mean DA %silt+clay (0.23.6%, $n = 4$) than did Zone A Tamarix sites (60.4%, $p = 0.017$, $df = 1,1$).

The %silt+clay in 1981 was significantly higher than that in 1984 on former *S. exigua* and open beach sites relative to substrate surface level (Table 2.3, Figure 2.2). This trend is opposite to that observed for %sand. In Zone D no significant change in texture was observed between years.

Regression of Zone A and B beach %silt+clay at 35cm depth with distance from Glen Canyon Dam produced a non-significant relationship in 1981 but a somewhat stronger relationship in 1984 ($R^2 = 0.374$; $p < 0.05$, $df = 1,7$; Table 2.5). Regression of the DA mean %silt+clay with distance from the dam also produced a moderately good correlation of these two variables in 1984 ($R^2 = 0.434$; $p < 0.05$, $df = 1,7$; Table 2.4).

The %silt+clay was uniformly minimal with respect to depth in Zone A profiles, but varied to a greater extent in Zone D profiles in 1984 (Figure 2.6). This is a reflection of the flood-induced disturbance sustained by Zone A substrates as compared to the undisturbed, interbedded laminar nature of Zone D substrates.

The correlation of %silt+clay against stage was weakly significant in 1981 ($R^2 = 0.179$; $p < 0.10$, $df = 1,15$), and improved greatly in 1984 ($R^2 = 0.512$; $p < 0.001$, $df = 1,18$; Table 2.6). This positive regression may be a function of flood-induced entrainment and/or tributary input.

Percent Clay

Using the Bouyoucos (1927) hydrometer method, the percent clay in samples was calculated for all 1984 samples (Table 2.1). These results are not directly comparable with the %sand and %silt+clay measurements made by sieving, yet they do corroborate the process of leaching and loss of fine particles that characterize the post-dam Colorado River riparian corridor. The grand mean DA %clay from all 20 sites in 1984 was 1.80% ($n=20$, Table 2.1). Former *Salix exigua* sites (all of which became open beach sites in 1984) had the lowest mean %clay, at 0.72% ($n=6$). Zone A *Tamarix* sites had 1.03% clay and open beach sites had 1.35% clay. None of these three cover types were significantly different from each other, yet their overall mean value of 0.945% clay was significantly lower than the Zone D sites (mean=3.57%, $n=6$) at $p=0.029$, $df=3,16$ (Table 2.2). *Tamarix* sites differed significantly between zones ($p=0.006$, $df=1,5$), with a Zone D mean of 3.17% ($n=3$). DA Zone A sites contained significantly lower %clay than did Zone D sites ($p = 0.001$, $df = 1,18$; Table 2.2).

Comparisons of %clay for matched 35cm depth samples collected in 1981 and 1984 show a significant reduction in %clay between years on all Zone A beach sites ($p = 0.023$, $df = 4$), relative to substrate surface level; but differences between years among vegetated Zone A sites and all Zone D sites were not statistically significant.

Scala's (op. cit.) data for 1981 showed a significant negative correlation between %clay at 35cm depth and distance from Glen Canyon Dam (Table 2.5). This correlation was not found for either the 35cm depth samples or the DA %clay data in 1984.

Scala's (op. cit.) 1981 %clay data from 35cm depth were not correlated with stage; however, 1984 data from 35cm showed a positive, statistically significant relationship with stage ($R^2 = 0.282$; $p < 0.01$, $df = 1,18$; Table 2.3).

During the pH analyses described above, Zone D sediments were commonly found to be hydrophobic, while inundated sediments from zones A and B were always non-hydrophobic. This observation may result from the higher clay content in Zone D sediments as compared to Zone A sediments.

In summary, the %sand in fluvial deposits along the Colorado River in Grand Canyon was highest in Zone A and lowest in Zone D. Distribution of %silt+clay particles followed precisely the opposite trend. Tamarix stands that persisted through the 1983 flooding event maintained higher proportions of silt and clay than did the sparsely vegetated and beach sites. The %sand at 35cm depth relative to the substrate surface increased significantly on Zone A beaches between 1981 and 1984, with a concomitant decrease in %silt/clay. Textural changes were particularly pronounced on sparsely vegetated sites. Densely vegetated sites in Zone A (e.g. Tamarix sites) experienced similar but non-significant trends in textural change. Non-inundated sites in Zone D showed no significant change in substrate texture between 1981 and 1984.

Discussion

Effects of Flooding on Edaphic Parameters

In the following section we discuss the significance of flood-induced changes in substrate characteristics, the effect of distance from Glen Canyon Dam, pedogenesis (soil evolution) through time, and the effects of substrate changes on present and future riparian vegetation in this system.

Substrate pH

Substrate pH reflects the influences of several environmental factors in this system. Soil pH generally declines as upper soils age, base cations are leached out, and as organic acids form (Birkeland 1984). Relatively high pH (approximately 8.1) near the surface indicates recent age near the river and/or slow rates of decomposition on pre-dam terraces, and is also indicative of the high carbonate concentrations in this system which probably buffer the substrate pH. Flooding homogenized substrate pH among the 4 cover types examined, relative to substrate surface level, and produced a significantly lower soil pH only on open beach sites in the inundated zone. In 1984 old high water zone substrates had a significantly lower DA pH than did new riparian zone sites. In the post-dam era, new riparian zone substrate pH appears to be decreasing slightly, approaching that of the river; pre-dam terrace pH values appear to be stable and somewhat lower. The pH of beach sands in Zone A may decrease slightly downstream from Glen Canyon Dam through time, and pH decreased slightly from the river's edge to the pre-dam terraces. The changes in substrate pH induced by flooding were relatively minor and probably do not significantly affect terrestrial vegetation in this system.

Base Cation Concentrations

Flooding/leaching reduced substrate cation concentrations among the 4 cover types examined, relative to substrate surface levels. Na^+ , K^+ , Ca^{2+} , and Mg^{2+} , as well as total cation concentrations, decreased significantly following flooding in all cases except for Mg^{2+} in the open beach cover type. Inundation of Tamarix sites significantly reduced monovalent cation concentrations, but divalent and total cation concentrations were not reduced significantly. Open beach sites and sites formerly occupied by Salix exigua showed significant declines in K^+ and in total cation concentrations. Non-inundated Zone D sites showed no significant change in cation concentrations between 1981 and 1984.

Analyses of variance of differences in cation concentrations between cover types and inundation zones showed that significant differences developed between cover types for all DA cation concentrations following flooding except highly soluble Na^+ . Differences among cover types were masked by data from the Tamarix sites, which lay in both Zone A and Zone D. Detailed analyses of changes on inundated versus non-inundated Tamarix sites revealed that decreases in monovalent and total cation concentrations relative to the surface level became significant and pronounced following flooding, while changes in divalent cation concentrations were non-significant. Differences between Zone A and Zone D also increased after flooding for all cations.

The Bureau of Reclamation conducted a test drop in the discharge levels during October 20-22, 1984, and one of us observed the effects of this test in Marble Canyon. Slumping and bank cutting were pronounced during this test drop in Marble Canyon, and large cracks developed in beach faces as water drained from them. The water seeping from beach faces smelled rank and "swampy", indicating that buried reduction environments were draining and changing to oxidizing environments. Reduction in the soil zone typically turns the substrate to a bluish color, and reduced soils are termed gleyed. Reduction of anoxic soils greatly increases the solubility of iron, manganese, and other cations (Birkeland 1984), and significant leaching of soil nutrients and minerals is likely to occur when discharge levels decline rapidly after a period of prolonged inundation. Capillary rise in sand and silt soils can lift water one to four meters depending on substrate texture (Birkeland 1984), and thus fluvial substrates are likely to be affected by the flow regime for a considerable distance from the river itself.

Organic Matter

Analysis of the percent of burnable organic matter + carbonates in 35cm depth samples indicates that organic matter is low to extremely low in this system and all substrates analyzed qualified as "mineral soils" in Allen's (1974) classification. Open beach sands contained little organic matter, Zone A Tamarix stands contained only slightly more, and Zone D sites contained a maximum of about 3%. Organic matter was apparently flushed from the system by flooding, particularly in the upper reaches, declining significantly in Zones A and B relative to substrate surface level, but not in Zone D from 1981 to 1984.

Texture

Our data show a significant increase in the %sand on Zone A beach sites relative to substrate surface level, particularly on sites that were revegetated by flooding in 1983. This trend was not noted by Beuss (pers. comm.); however, his sampling program differed from ours in intent. Beuss sampled at absolute levels to determine deposition and/or erosion, while we sampled at the surface to evaluate changes in substrate conditions for existing and potential vegetation. Other differences between the two sampling programs were that Beuss's samples were taken from open, previously unvegetated beaches in which our data also show non-significant between-year textural changes; and his samples were taken from beaches heavily used by recreationists.

The relative increase in %sand in post 1983 Zone A and B riparian sediments will probably result in increased susceptibility to erosion, increased leaching rates, and decreased moisture retention. Leaching removes soil cations, organic matter, and may eventually lead to decreased pH (Birkland 1984). During 1984 and 1985, relatively high levels of discharge kept riparian sediments moist, creating reducing soil environments at depth in several of the profiles sampled. A return to "normal" post-dam discharges of less than $800\text{m}^3/\text{sec}$ in this system will cause dehydration of the substrate, perhaps leaving many seedling riparian plants without sufficient moisture. This aspect will be examined in 1986 by one of us (Waring).

In summary, it is clear that the redeposited beaches formed as a result of flooding in 1983 are, in fact, new beaches with significantly different chemical and physical properties than their predecessors. We have documented pronounced declines in base cation concentrations (especially monovalent cations) and in the proportion of fine-particle silts and clays in the profiles examined relative to substrate surface level. Flooding/leaching in 1983 and 1984 significantly reduced base cation concentrations except Mg^{2+} ; total cation concentration decreased significantly; the proportion of burnable organic matter+carbonates declined significantly; substrate texture became significantly more coarse except where it was protected by dense stands of Tamarix; and pH remained relatively unchanged, probably as a consequence of the buffering effects afforded by elevated soil carbonate concentrations in this system. At the present time riparian substrates in the inundated riparian corridor of the Colorado River in Grand Canyon are typified by pH values of approximately 8.0; low concentrations of monovalent Na^+ ($40.1\mu\text{g/g}$) and K^+ ($25.9\mu\text{g/g}$) and relatively high concentrations of divalent Ca^{2+} ($1314\mu\text{g/g}$) and Mg^{2+} ($208.0\mu\text{g/g}$); extremely low organic content ($<0.37\%$); and a sand texture (89% sand, approximately 9.5 %silt, and less than 1% clay).

Effect of Distance from the Dam on Edaphic Parameters

Regression of edaphic parameters against distance from Glen Canyon Dam resulted in several trends. The pH of samples was not correlated with distance in either 1981 or 1984 35cm-depth samples, or in 1984 DA samples. Substrate pH is largely a function of ion composition, ion concentration, and organic content (organic matter produces organic acids), and is buffered by high concentrations of carbonates. Thus it is not particularly surprising to find the pH of these high carbonate,

low organic content sediments relatively uniform throughout the Colorado River riparian corridor.

Regression analyses of DA base cation concentrations against distance (Table 2.4) showed significant positive correlations between Ca^{2+} and total cation concentrations with distance downstream in 1984. Ca^{2+} comprised nearly 80% of the total cation concentration, thus these variables are strongly intercorrelated. Despite correlations of K^+ concentration at 35cm depth with distance from the dam in 1981 and 1984, DA concentrations of these other three cations did not correlate with distance.

The DA percent burnable organic matter + carbonates showed a significant, positive relationship with distance from the dam. Because this relationship did not exist in 1981, and because 1981 values were significantly and far higher than 1984 values, we conclude that flooding removed organic materials in the upper Canyon to a greater extent than it did in the lower Canyon.

Linear regression analysis revealed a significant decrease in the %sand and a converse increase in the %silt+clay in open beach substrates with distance downstream from Glen Canyon Dam in 1984. In other words, beaches in upper Grand Canyon contained significantly more sand-sized sediments, and those in lower Grand Canyon contained more silt and clay. This may be attributed to redeposition of sand in the lower Canyon and higher rate and period of entrainment of fine particles over coarse particles. From our data we could not determine which process is more important; however, other researchers in this environmental assessment are studying sediment transport and depositional processes and should clarify these details.

In summary, distance from Glen Canyon Dam was positively correlated with Ca^{2+} and total base cation concentrations, %organic matter + carbonates, and %silt + clay, and distance was negatively correlated with %sand. These results suggest that flooding exerted a greater impact on terrestrial riparian substrates in the upper reaches, and that flood related impacts in the lower Canyon may be obscured by tributary influences.

Pedogenesis

Under natural conditions, soils in this system age rather slowly. The pre-dam silts and clays sampled appeared extremely dry, contained little organic matter, and generally showed little pedogenic development. This is clearly illustrated by the relatively great age of one pre-dam terrace sample from 100cm depth at Mile 198.5R, which showed no signs of weathering, yet had a ^{14}C age of ca. 450 + 50 years (A.K. Behrensmeyer pers. comm. 1985) and a relatively high pH (8.3). In part this retarded soil development must be attributed to the impermeability of silt and clays to meteoric water. In August, 1982 precipitation from a hard, soaking rain was found to percolate at the rate of less than 1.0cm/hour, and reached only 15cm depth in beach-sand soil.

To address the question of pedogenic trends in post-dam riparian substrates through time, refer to Table 2.6 and Figures 2.2 and 2.3.

These data show that the differences between inundated Zone A and non-inundated Zone D sites increased among all edaphic parameters between 1981 and 1984. Prior to flooding in 1983, the riverside Zone A substrates were physically and chemically more similar to the pre-dam Zone D sediments than they are at present. It is unfortunate that we do not have samples of Zone A sediments from the late pre-dam or early post-dam era. Pre-dam Zone A sediments were probably similar but not identical to present-day Zone D sediments. The pre-dam Zone A sediments were probably fine-textured and relatively rich in base cations and perhaps soil nutrients as well. From 1963 to 1981 a significant decrease in monovalent cation and total cation concentrations occurred, and possibly a significant increase in %sand developed in Zone A sediments, relative to Zone D. In 1984 all parameters studied except pH were significantly correlated with stage, and the significance of those relationships that were significant in 1981 improved greatly. From these observations we suggest that the post-dam riparian edaphic system has changed slowly under a stable flow regime, and changed abruptly with the re-initiation of extreme discharges in 1983.

Edaphic Changes and Riparian Vegetation

Flooding in 1983 and 1984 altered substrate characteristics in Zones A and B of the Colorado River riparian corridor by scouring and leaching base cations, organic matter, and fine particle silts and clays. Prior to flooding, levels of these substances were generally closer to those of the pre-dam terraces, and organic matter from root decay and leaf litter had been accumulating. After 1983 lower concentrations of exchangeable cations, lower levels of organic matter, and higher proportions of larger-sized particles were observed, relative to the substrate surface level, and these changes are generally considered detrimental to the growth of riparian vegetation.

Analysis of matched photographs conducted by Turner and Karpiscak (1980) has shown a relatively rapid proliferation of riparian vegetation in this system from 1963 to 1975. This proliferation has been somewhat ordered by flooding, with recruitment following subsidence of flood waters (e.g. Hayden 1976), and subsequent development of community complexity (e.g. Brian 1982). Invasion of this system by Tamarix in Zone A occurred in the late 1960's and early 1970's. Phillips (in Brian op. cit.) claimed that the first decade of regulated flow in this system was characterized by erosion which prevented plant community development; however, the effects of disturbance in 1965 may have facilitated recruitment in this system. In the present study we found that dense Tamarix stands are resistant to scouring and retain silt and clay particles, base cations, and organic matter more effectively than do the native plant species. Therefore Tamarix is important in this system where it serves to stabilize the substrate.

Declines in substrate quality will occur with every major flood in this system. To maximize development of the terrestrial riparian community, a stable, non-flooding flow regime would permit the greatest amount of pedogenesis. Many of the current beaches in this system formed at about the $800\text{m}^3/\text{sec}$ stage as a consequence of prolonged flows greater than $1,100\text{m}^3/\text{sec}$ from 1983 to 1985. To permit new beaches to undergo pedogenesis, the flow regime adopted should be one which minimizes bank-

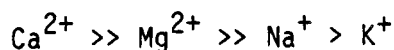
cutting erosion (e.g. a stable, base-loaded flow or a flow regime with mild, slow fluctuations) or should not exceed a relatively low long-term mean maximum discharge of less than $800\text{m}^3/\text{sec}$. Such a flow regime would maximize pedogenic development by permitting recolonization by vegetation, accumulation of organic matter, and would retard leaching of base cations and fine particles. Choice of a suitable flow regime will determine substrate evolution and, consequently, riparian vegetational development in this system.

Conclusions

Several conclusions are drawn from this portion of the study study:

1. Sampling sites that lay within the inundation zone of the 1983 flooding event were altered by moderate to extreme devegetation, scouring of the substrate, and in some cases redeposition of fluvial sediments.

2. In 1984 this system was characterized by young, unweathered xerifluventic substrates with moderately high pH, low organic content, fine silt/sand textures, and base cation ratios of:



3. Samples collected in 1984 revealed significant changes in physical and chemical substrate characteristics, relative to substrate surface level, as compared to samples collected before flooding in 1981:

- a) Substrate pH differences between various cover types in the inundated zone were more homogenous.
- b) Monovalent and, to a lesser extent, divalent base cation concentrations (except Mg^{2+}) declined significantly in the inundated zone between years. Cation concentration differences between the inundated and non-inundated zone became more pronounced following flooding.
- c) The percent burnable organic matter + carbonates declined significantly in the inundated zone as a consequence of flooding.
- d) The percent sand in the inundated zone increased and the %silt+clay decreased significantly as a result of flooding

4. Correlation of substrate characteristics with distance from Glen Canyon Dam was significant and positive for Ca^{2+} concentrations as well as percent burnable organics + carbonates and percent silt + clay. These relationships may be attributed to increased scouring near the dam with redeposition in the lower Grand Canyon and/or the influence of tributaries in this system.

5. All physical and chemical substrate characteristics at 35cm depth were more strongly correlated with stage in 1984 than in 1981, reflecting the impact of flooding on riparian substrates.

6. Analyses of substrate characteristics with respect to depth in the profile corroborated Scala's (op. cit.) findings that pre-dam sediments consist of interbedded laminae of fine silts, fine sands, and mixed

texture substrates. This pattern was significantly altered by scouring and redeposition in 1983 at numerous sites. Base cation analyses showed that the "bulges" in concentrations found in pre-dam sediments were lower and less conspicuous in the profiles of post-1983 sample sites for all species except K^+ , which was strongly leached from this system.

7. These changes in physical and chemical substrate characteristics represent a significant deterioration in environmental conditions for surviving and future riparian plant life in the inundation zone. In particular, the increase in particle size of beach sediments in this system may lead to increased erosion rates and more rapid desiccation of the substrate, conditions highly unfavorable to colonizing plants.

8. Among the inundated sites, substrate quality beneath exotic Tamarix stands was consistently better than that associated with native Salix exigua stands or open beach sites. Reasons for this include the following: Tamarix stands typically occupy erosion-resistant pre-dam silt beds, and Tamarix is more deeply rooted and protects the substrate from flood-induced scouring better than Salix does.

9. Pedogenesis of riparian substrates is a slow process, one facilitated by the growth of vegetation and negatively affected by flooding and other environmental disturbances. Maintenance or improvement of riparian substrate quality will require concerned, consistent management in this system.

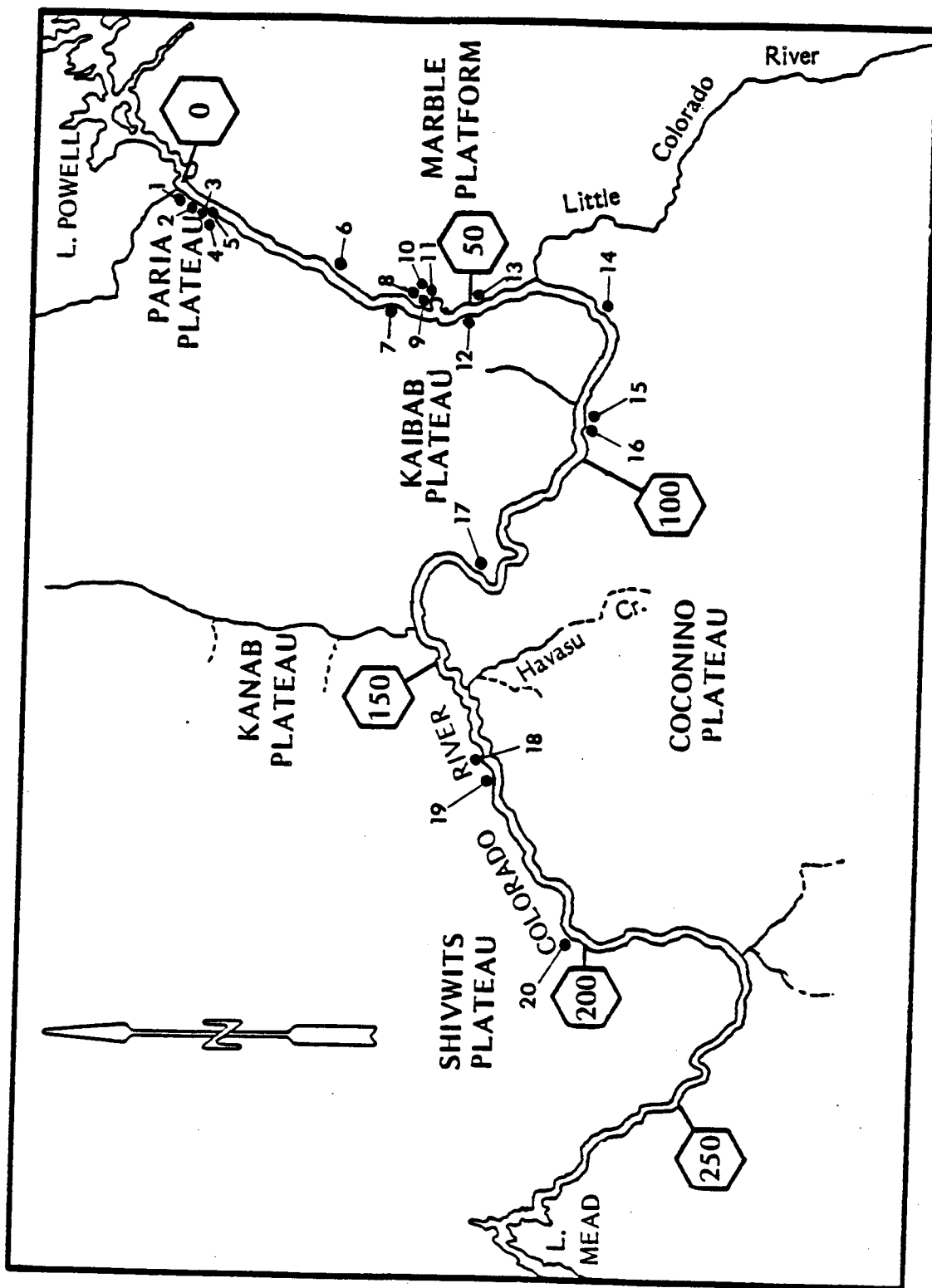


FIGURE 2.1: COLLECTION SITES FOR RIPARIAN SUBSTRATE SURVEY IN GRAND CANYON, 1984.

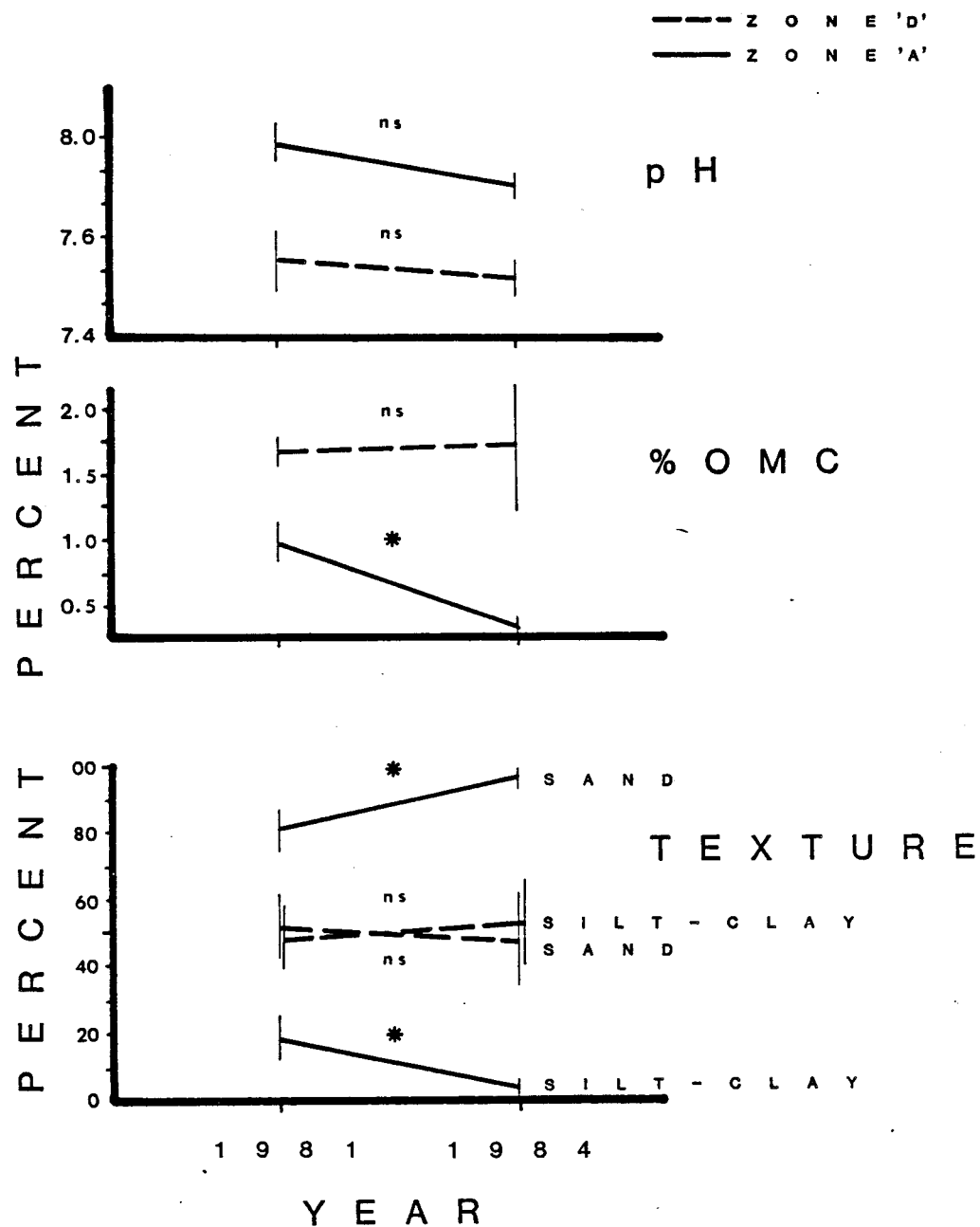


FIGURE 2.2: SUBSTRATE pH, % ORGANIC MATTER + CARBONATES, AND TEXTURE (%SAND AND %SILT + CLAY) FROM 1981 TO 1984 AT 35CM DEPTH RELATIVE TO THE SURFACE LEVEL AT THE TIME OF SAMPLING, IN INUNDATED ZONE A (EXCLUDING TAMARIX SITES) AND NON-INUNDATED ZONE D.

--- N O N I N U N D A T E D
 — I N U N D A T E D

TOTAL BASE CATIONS

Ca^{2+}

Mg^{2+}

Na^+

K^+

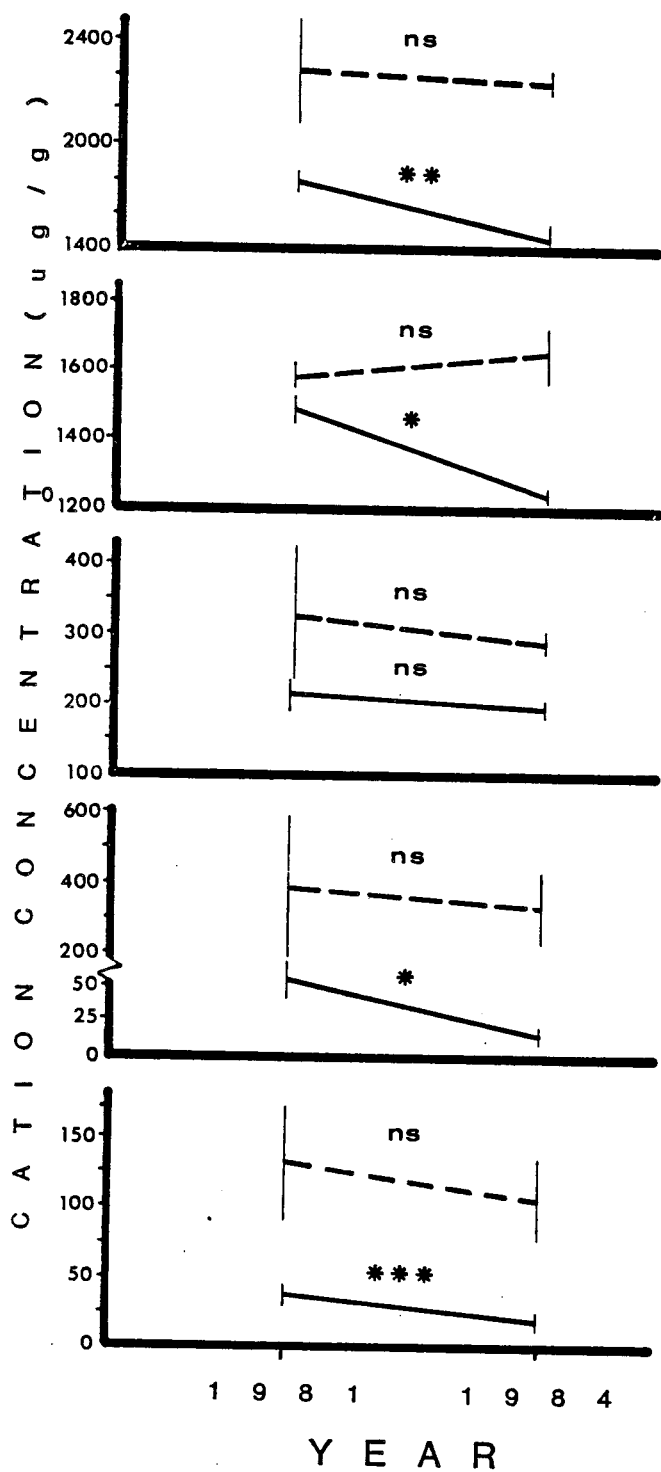


FIGURE 2.3: BASE CATION CONCENTRATIONS FROM 1981 TO 1984 AT 35CM DEPTH RELATIVE TO THE SURFACE LEVEL AT THE TIME OF SAMPLING, IN INUNDATED ZONE A (EXCLUDING TAMARIX SITES) AND NON-INUNDATED ZONE D.

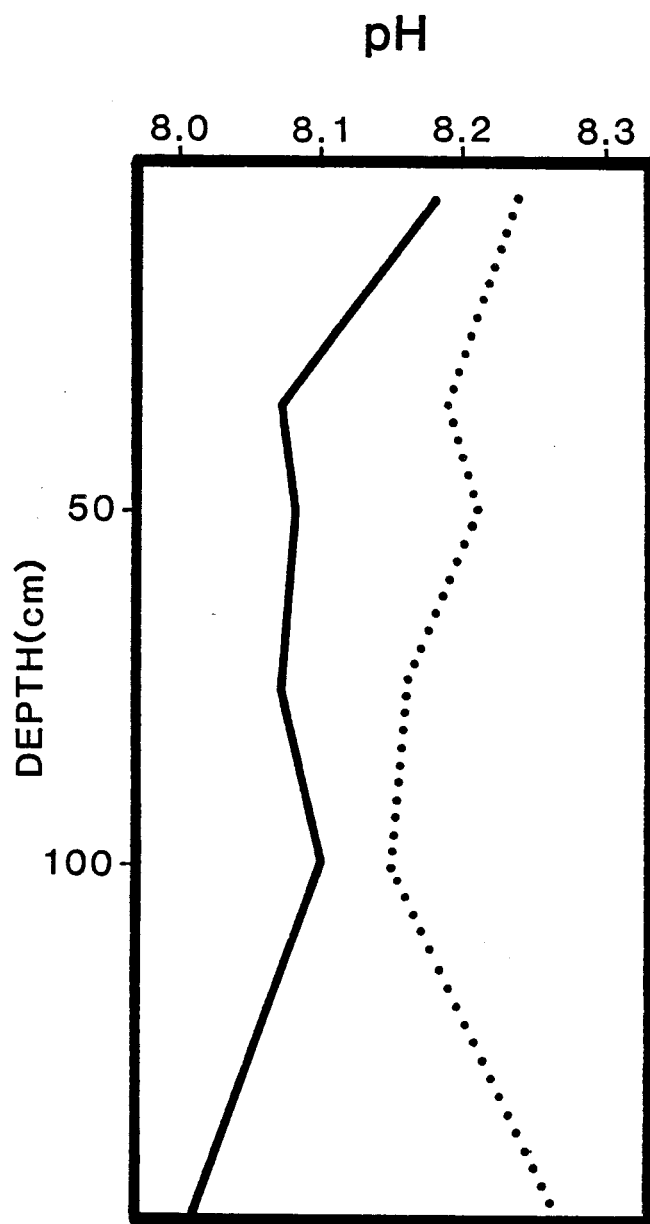


FIGURE 2.4: SUBSTRATE pH THROUGH DEPTH IN 1984 FOR INUNDATED ZONE A (DOTTED LINE) AND NON-INUNDATED ZONE D (SOLID LINE). DATA FROM TAMARIX SITES IN ZONE A WERE EXCLUDED. VALUES ARE MEANS.

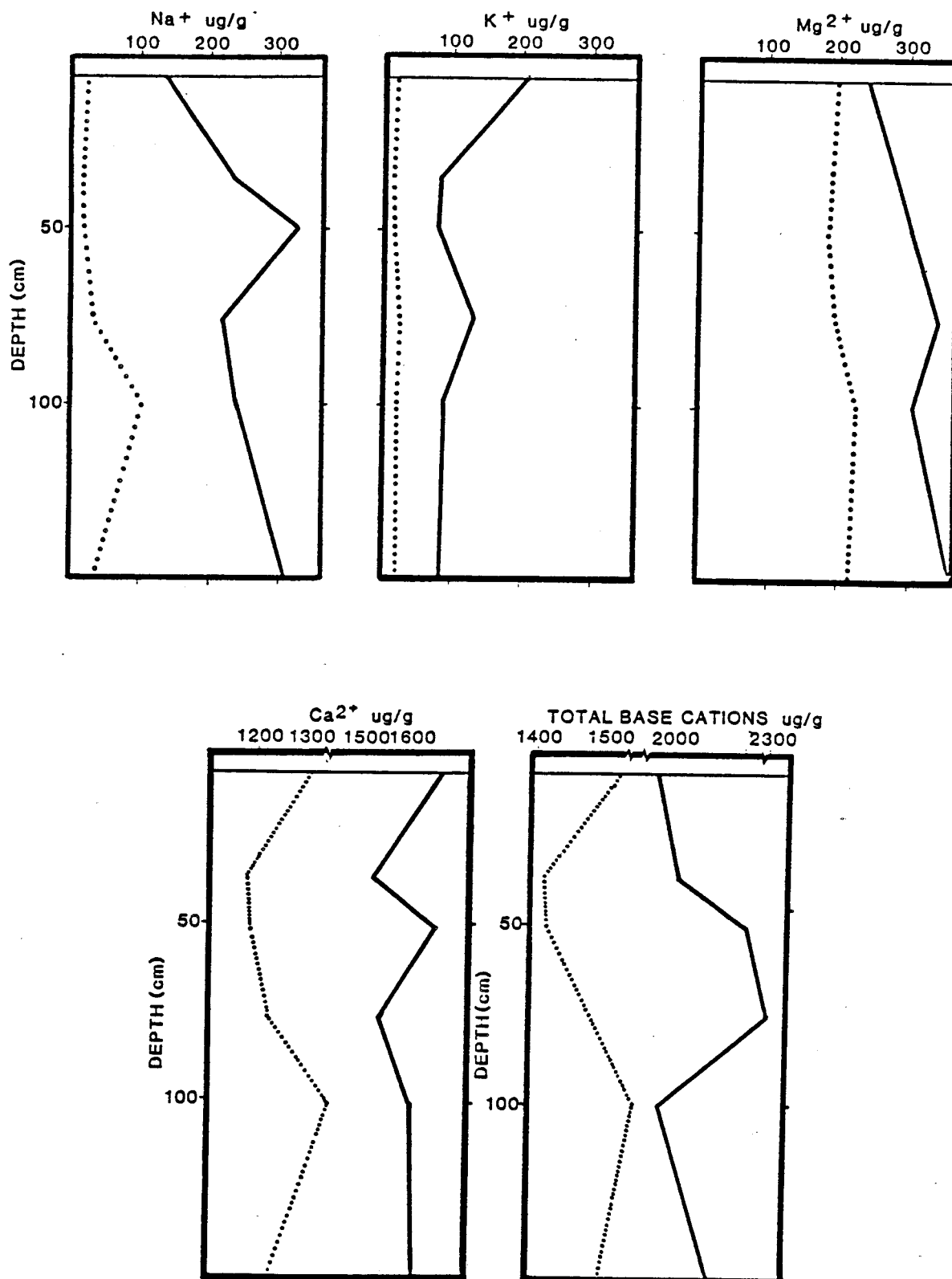


FIGURE 2.5: MEAN BASE CATION CONCENTRATIONS BY DEPTH FROM POOLED ZONE A SITES ((DOTTED LINES) AND ZONE D SITES (HEAVY LINE) IN 1984. SEE TEXT FOR STATISTICS.

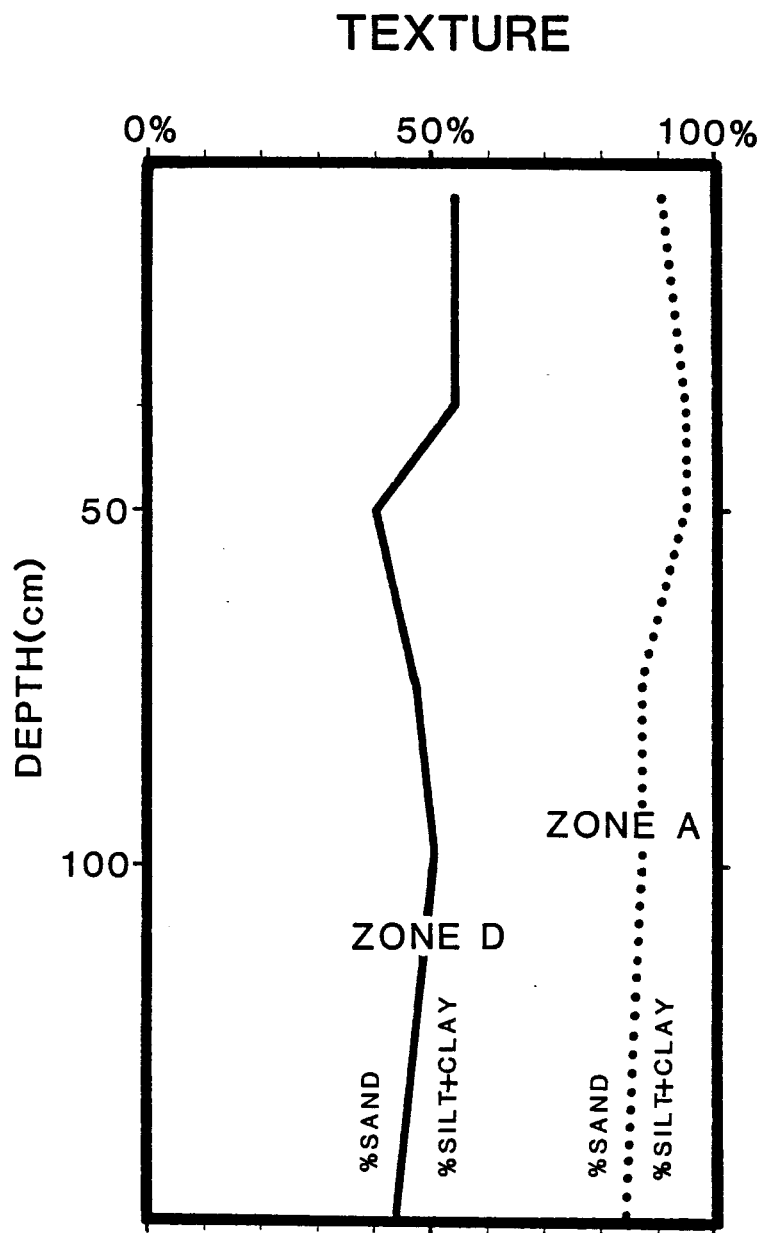


FIGURE 2.6: SUBSTRATE TEXTURE (%SAND AND %SILT + CLAY) THROUGH DEPTH IN 1984 IN INUNDATED ZONE A (EXCLUDING TAMARIX SITES) AND NON-INUNDATED ZONE D. VALUES ARE MEANS.

TABLE 2.2: SUMMARY OF STATISTICAL SIMILARITY OF 1984 PHYSICAL AND CHEMICAL SUBSTRATE CHARACTERISTICS BETWEEN COVER TYPES AND INUNDATION ZONES USING ANALYSIS OF VARIANCES AND DUNCAN'S MULTIPLE RANGE TEST WITH $p < 0.05$. LETTERS DENOTE STATISTICAL SIMILARITY WITHIN GROUPS.

EDAPHIC PARAMETER	STATISTICAL SIGNIFICANCE OF DIFFERENCES BETWEEN COVER TYPES (df = 3,16)	COVER TYPES				STATISTICAL SIGNIFICANCE OF DIFFERENCES BETWEEN ZONE A+B AND ZONE D SITES (df = 1,18)
		OPEN BEACH (df = 5)	SALIX EXIGUA (df = 4)	TAMARIX (df = 4)	ALL ZONE D SITES (df = 6)	
pH	p = 0.051	a	a	ab	b	p = 0.025
Na ⁺ (ug/g)	p = 0.193	a	a	a	a	p = 0.004
K ⁺ (ug/g)	p < 0.001	a	a	b	c	p < 0.001
Ca ²⁺ (ug/g)	p = 0.001	a	a	b	b	p = 0.002
Mg ²⁺ (ug/g)	p = 0.012	a	a	b	b	p = 0.002
TOTAL CATIONS (ug/g)	p = 0.002	a	a	b	b	p < 0.001
% ORGANIC & CARBONATES	p = 0.076	a	a	ab	b	p < 0.001
% SAND	p = 0.001	a	a	b	b	p < 0.001
% SILT AND CLAY	p = 0.002	a	a	b	b	p < 0.001
% CLAY	p = 0.029	a	a	a	b	p < 0.001

TABLE 2.4 : LINEAR REGRESSION EQUATIONS OF 1984 DEPTH-AVERAGED
PHYSICAL AND CHEMICAL SUBSTRATE CHARACTERISTICS
AGAINST DISTANCE DOWNSTREAM FROM GLEN CANYON DAM,
USING ZONE A AND B BEACHES.

SOIL PARAMETER	REGRESSION EQUATION	R ² VALUE (ADJ. FOR df)	SIGNIFICANCE (df)
pH	$Y = -0.001X + 8.30$	0.000	NS (1,7)
Na ⁺ (ug/g)	$Y = 0.268X + 18.5$	0.000	NS (1,7)
K ⁺ (ug/g)	$Y = 0.082X + 13.9$	0.025	NS (1,7)
Ca ²⁺ (ug/g)	$Y = 2.740X + 1089$	0.478	p < 0.05 (1,7)
Mg ²⁺ (ug/g)	$Y = 0.316X + 172$	0.101	NS (1,7)
TOTAL CATIONS (ug/g)	$Y = 3.400X + 1293$	0.455	p < 0.05 (1,7)
* % ORGANIC & CARBONATES	$Y = 0.003X + 0.130$	0.512	p < 0.05 (1,7)
% SAND	$Y = -0.139X + 103$	0.434	p < 0.05 (1,7)
% SILT & CLAY	$Y = 0.139X + 2.83$	0.434	p < 0.05 (1,7)
% CLAY	$Y = 0.006X + 0.40$	0.029	NS (1,7)

* 35cm depth only

TABLE 2.5: LINEAR REGRESSION EQUATIONS OF PHYSICAL AND CHEMICAL SUBSTRATE CHARACTERISTICS AGAINST DISTANCE DOWNSTREAM FROM GLEN CANYON DAM, USING ZONE A AND B BEACHES IN 1981 AND 1984 AT 35CM DEPTH.

PARAMETER	YEAR	REGRESSION EQUATION	R ² VALUE (ADJ. FOR df)	SIGNIFICANCE (df)
pH	1981	Y = 0.001X + 8.01	0.000	NS (1,6)
	1984	Y = -0.002X + 8.20	0.131	NS (1,7)
Na ⁺ (ug/g)	1981	Y = 0.514X + 10.8	0.127	NS (1,6)
	1984	Y = 0.088X + 9.96	0.232	NS (1,7)
K ⁺ (ug/g)	1981	Y = 0.228X + 15.3	0.671	p<0.01(1,6)
	1984	Y = 0.071X + 9.05	0.415	p<0.05(1,7)
Ca ²⁺ (ug/g)	1981	Y = -0.703X + 1542	0.000	NS (1,6)
	1984	Y = 1.260X + 1142	0.000	NS (1,7)
Mg ²⁺ (ug/g)	1981	Y = 0.305X + 183	0.000	NS (1,6)
	1984	Y = 0.009X + 183	0.000	NS (1,7)
TOTAL CATIONS(ug/g)	1981	Y = 2.100X + 1522	0.261	NS (1,6)
	1984	Y = 0.580X + 1417	0.099	NS (1,7)
% ORGANIC+ CARBONATES	1981	Y = -0.001X + 1.18	0.000	NS (1,5)
	1981	Y = 0.003X + 0.136	0.513	p<0.05(1,8)
% SAND	1981	Y = -0.097X + 88.8	0.000	NS (1,6)
	1984	Y = -0.075X + 102	0.378	p<0.05(1,7)
% SILT+CLAY	1981	Y = 0.097X + 11.3	0.000	NS (1,6)
	1984	Y = 0.074X - 1.63	0.374	p<0.05(1,7)
% CLAY	1981*	Y = -0.030X + 5.79	0.668	p<0.01 (1,6)
	1984	Y = 0.001X + 0.504	0.000	NS (1,8)

TABLE 2.6 : LINEAR REGRESSION EQUATIONS OF PHYSICAL AND CHEMICAL
SUBSTRATE CHARACTERISTICS AGAINST APPROXIMATE STAGE
OF SAMPLE SITE IN 1981 and 1984 AT 35CM DEPTH.

PARAMETER	YEAR	REGRESSION EQUATION	R ² VALUE (ADJ. FOR df)	SIGNIFICANCE (df)
pH	1981	Y = -0.001X + 8.1	0.129	p < 0.10 (1,15)
	1984	Y = -0.001X + 8.06	0.115	p < 0.10 (1,18)
Na ⁺ (ug/g)	1981	Y = 0.119X - 64.5	0.266	p < 0.025(1,15)
	1984	Y = 0.083X - 55.5	0.378	p < 0.005(1,18)
K ⁺ (ug/g)	1981	Y = 0.035X - 1.1	0.478	p < 0.005(1,15)
	1984	Y = 0.030X - 14.1	0.604	p < 0.001(1,18)
Ca ²⁺ (ug/g)	1981	Y = 0.052X + 1399	0.103	NS (1,15)
	1984	Y = 0.113X + 1178	0.253	p < 0.025(1,18)
Mg ²⁺ (ug/g)	1981	Y = 0.035X + 184	0.079	NS (1,15)
	1984	Y = 0.028X + 169	0.332	p < 0.005(1,18)
TOTAL CAT- IONS(ug/g)	1981	Y = 0.242X + 1518	0.402	p < 0.005(1,15)
	1984	Y = 0.254X + 1277	0.515	p < 0.001(1,18)
% ORGANIC+ CARBONATES	1981	Y = 0.001X + 1.08	0.000	NS (1,12)
	1984	Y = 0.001X - 0.203	0.565	p < 0.001(1,18)
% SAND	1981	Y = -0.009X + 87.1	0.178	p < 0.05 (1,15)
	1984	Y = -0.016X + 107	0.511	p < 0.001(1,18)
% SILT+CLAY	1981	Y = 0.009X + 13.0	0.179	p < 0.10 (1,15)
	1984	Y = 0.016X - 7.37	0.512	p < 0.001(1,18)
% CLAY	1981	Y = 0.001X + 3.74	0.000	NS (1,12)
	1984	Y = 0.002X - 1.38	0.282	p < 0.01 (1,18)

CHAPTER III: EFFECTS OF FLOODING ON RIPARIAN VEGETATION

Introduction

Flooding is the most ubiquitous form of disturbance in riparian ecosystems. In unregulated stream systems, flooding mechanically controls riparian plant community development and may initiate repetitive waves of succession (Loucks 1970; McIntosh 1980), which result in a "suspended succession" (Campbell and Green 1968). Odum (1981) suggested that periodic perturbations result in lower levels of biological organization (i.e. diversity and complexity of trophic structure). Catastrophic disturbance lowers the "trajectory of ecological succession" by direct reduction of biomass and diversity, temporarily returning the ecosystem to an earlier stage of development. A change in the perturbation regime may change the course of succession by eliminating some biotic interactions while forcing or promoting others.

Numerous factors influence flood-related plant mortality. Mortality varies with plant age and between species, and inundation resistance increases with plant age (Hosner 1958; Horton et al. 1960; Warren and Turner 1975; Kozlowski 1984). Prolonged flooding negatively affects leaf, shoot, cambial and root growth and morphology, and successful seedling establishment varies widely between plant species following flooding (Kozlowski 1984). Abiotic factors that influence plant mortality include water temperature, oxygen depletion and other changes in inundated soils (Ponnamperuma 1984), duration and discharge level, and turbidity which reduces light availability for inundated plants.

Discharge regulation (flood control) permits plant life to colonize streambanks and creates ecologically and recreationally valuable riparian habitat (Johnson and Jones 1977; Johnson and Carothers 1982; Johnson et al. 1985); however, flooding events subsequent to discharge regulation negatively affect riparian plant communities through damage and mortality of streamside plants. Such has been the case along the Colorado River corridor in Grand Canyon, Arizona. Little riparian vegetation existed along the river prior to construction of Glen Canyon Dam (Turner and Karpiscak 1980). From 1963 to 1982 discharge was stabilized below approximately about $820\text{m}^3/\text{sec}$, providing a new habitat that was gradually colonized by exotic and native plant species. This convention was interrupted in 1983, when inflow to Lake Powell exceeded the storage capacity of Glen Canyon Dam. On 29 June, 1983 discharge from Glen Canyon Dam increased to $2,621\text{m}^3/\text{sec}$, sending the highest flow in post-dam (post-1963) history through the Colorado River corridor in Grand Canyon. Mean discharge remained above $680\text{m}^3/\text{sec}$, twice the normal flow level through 1984, and exceeded $1,270\text{m}^3/\text{sec}$ in 1985, far above the pre-established normal flow. This severe and prolonged flooding has exerted significant impacts on the riparian plant community in the Colorado River corridor in Grand Canyon.

From the standpoint of the various species of riparian plants in this system, the flooding events of 1983, 1984, and 1985 were not "natural" events. These floods consisted of prolonged, constant flows of clear,

extremely cold water. "Natural" floods in this system are of two kinds: 1) sediment-laden spring and summer snowmelt discharge that warmed progressively through the year, and 2) ephemeral, high intensity tributary floods of warm, sediment-laden water. Type 1 (pre-dam river) floods scour and drown riverside vegetation, and represent a form of ecological disturbance to which terrestrial plant species are unable to adapt. Type 2 floods (flash floods) are usually of sufficiently short duration to prevent drowning of plants and many native and exotic species survive such flooding events.

Objectives

By permitting flooding in a system where erratic discharges had been stabilized for two decades, the operation of Glen Canyon Dam directly reduced terrestrial riparian vegetation and wildlife community along the Colorado River in Grand Canyon 1983. In the present study we document the impact of this flooding event on the riparian plant community in the Colorado River corridor in Grand Canyon. We posed the following questions regarding the impacts of flooding in this system:

- 1) What are the flood-related sources of plant mortality in this system?
- 2) Do all riparian plant species respond to flooding in a similar fashion in this system?
- 3) Do discharge stage, reach type, substrate type, distance from Glen Canyon Dam, stem density, and/or stem height influence flood-induced plant mortality?
- 4) How was plant growth affected by flooding during and after these discharges?
- 5) How do different plant growth and reproductive strategies (e.g. sexual versus clonal strategies) affect survival and recovery?
- 6) Did flooding result in increased germination and seedling establishment in 1984 and 1985?
- 7) Did flooding increase exposure and insolation of the substrate beneath stands of riparian vegetation?
- 8) Did riparian plant diversity and community structure change as a result of the 1983 flooding event, and what are the long-range consequences of such flooding events in this system?

In the following discussion we address these questions from the perspective of how the operation of Glen Canyon Dam has affected terrestrial vegetation along the Colorado River in Grand Canyon.

Methods

An inspection of the river corridor in the fall of 1983 revealed three sources of flood-induced plant mortality. These were 1) direct removal of plants by scouring; 2) drowning under prolonged flows; and 3) burial under redeposited fluvial sediments.

To assess levels of removal, mortality data were collected from several sources. River-based surveys of the riparian corridor from 1983 through 1985 provided three sets of removal data (Appendix 3.2). The presence and condition of plants that had been under observation since 1980 were determined in 1984 following the subsidence of flows $>700\text{m}^3/\text{sec}$. Several reaches were censused by counting all shrubs and trees visible from the river in 1982 and 1984, especially between miles 60-61, miles 166.5-179.5 (for *Prosopis* only), and miles 196.5-198.0. Nine $10\text{m} \times 30\text{-}40\text{m}$ study sites, each situated with its long axis parallel to the river and less than 5m from the $700\text{m}^3/\text{sec}$ stage were censused. These study sites were located between miles 43 and 170 (downstream from Lees Ferry) and were sampled for plant density and species composition in 1982 and 1985. Lastly, a small set of pre-1983 aerial photographs was ground-truthed in 1984 to ascertain removal of *Tamarix* in riffle and rapid reaches where few other data were available. Information gathered from all sources included plant species, height, and condition, with independent stems and distinct clumps considered as single individuals. The proximity of plants to the river (a measure of the period of inundation) was determined by dividing the total inundated area into three floodzones, all of which lay in Carothers et al. (1979) Zones 3 and 4: Zone A = $570\text{m}^3/\text{sec}$ to $1,130\text{m}^3/\text{sec}$; Zone B = $1,130\text{m}^3/\text{sec}$ to $1,700\text{m}^3/\text{sec}$; and Zone C = $1,700\text{m}^3/\text{sec}$ to $2,400\text{m}^3/\text{sec}$. Zone D lay in the non-inundated zone above $2,400\text{m}^3/\text{sec}$. Reach type categories included eddy, straight, riffle, or rapid settings. Substrate types included silt, sand, mixed sand and cobble, cobble, and bedrock. Distance downstream from Glen Canyon Dam was recorded from Stevens (1984). Because almost all of the post-dam riparian vegetation occurred below the $1,700\text{m}^3/\text{sec}$ stage, data on plants larger than the seedling sizes from the Zones A and B were pooled for analysis of removal. Removal rates were averaged by technique to obtain a total removal rate by species. χ^2 analyses with the Yates correction for continuity (Brower and Zar 1977) were used to determine if removal was significant for each species.

Mortality due to drowning of all perennial riparian species was derived from several data sets. Mortality was measured on 47 quadrats in 1984, and 12 of these quadrats were censused again in 1985 (Figure 3.1). Quadrat sites were selected in the four reach types throughout the river corridor. Each quadrat was 30m in length and extended to the top of Zone C. The number and heights of live and dead plants (including seedlings) of each species were measured in each zone of each quadrat, and quadrat width was measured. Thus, all plants on more than 3.68 ha of riparian habitat were examined in 1984 in quadrat analyses. Unflooded Zone D was not an appropriate control area against which to compare the inundated zones because growing conditions and sources of mortality were different there. Another set of mortality data was derived by counting all plants growing along the river in specific

reaches in 1982 and 1984, including Miles 60 to 61 (left side only), Mile 166.5 to 179.0 (right side, Prosopis only), Mile 196.0 to 198.0 (right side only), and elsewhere (Appendix 3.2). Mortality data were also derived from study plot analyses, observations on the survivorship of plants under observation since 1980, and by ground-truthing a small set of pre-1983 aerial photographs of the river corridor supplied by the National Park Service staff at Grand Canyon. Mortality was averaged across techniques to obtain a mortality rate by species. Data were analyzed using χ^2 statistics, multiple linear regression and analyses of variance (Snedecor and Cochran 1980).

The effects of burial were assessed by observation on the condition of individuals of different plant species throughout the river corridor. Mortality due to burial by newly deposited beach sediments could not be distinguished from drowning; however, plant species were observed to respond differentially to this source of mortality. To assess the effects of flood-related burial on plant growth we marked one stem on 20 buried and 20 unburied living Tamarix plants at Mile 205.0L, and remeasured marked stems in late June, 1985.

The effects of distance from Glen Canyon Dam, reach type, substrate type, and stem height on plant mortality due to drowning were assessed using quadrat data. Analyses of variance of mortality with these location and position factors were performed using BMDP statistical programs (Dixon 1983).

Removal of riparian vegetation may increase insolation of beach surfaces and increased light intensity may, in turn, influence seedling success. To gain some understanding of flood-related changes in light intensity in this system we compared light intensity in heavily damaged versus undamaged stands of Salix exigua (2 pairs) and Tamarix (4 pairs). Light intensity was measured with a Gossen foot-candle meter at 0.85m above the beach surface every 5.0m along a 35m-transect through uniform stands of vegetation. Light intensity was expressed as the percentage of ambient light.

To assess changes in vegetation diversity and community structure in this system, we calculated Shannon and Wiener's H' index of diversity and Pielou's J , a coefficient of evenness (Brower and Zar 1977):

$$H' = - \sum p_i (\log_{10} p_i)$$

$$J' = H' / \log_{10} S$$

where p_i is the proportion of species i in the sample and S is the number of species. H' is relatively independent of sample size and combines abundance and species richness species into a single, relative measure of diversity. H' varies from 0 for non-diverse communities to 1.0 for highly diverse communities. J' is a measure of evenness of distribution of species in a community and varies from 0 for highly unevenly distributed species to 1.0 when all species are equally represented. Both of these statistics were calculated using 1984 data from 6 quadrats in each of 4 reach types for the common riparian perennial species ($n=24$). Estimated pre-flood community diversity was

calculated using the number of live and dead stems of each species divided by the total number of stems of all species (by not correcting these values for removal we ensured that our pre-flood estimates were conservative). Post-1983 community diversity statistics were calculated using the number of live stems of each species divided by the total number of live stems of all species. H' and J' values were compared between years and reach types using Student's t statistics and oneway analysis of variance.

Results

Plant Mortality Prior to 1983

In general, nearly all plants encountered in Zones A and B were growing vigorously in 1982, with mortality levels less than 5%. Low density stands of plants revealed low levels of stem mortality levels prior to 1983. For example, mortality levels for Tamarix, Prosopis, and Baccharis species were 1.9% ($n=494$), 2.2% ($n=45$), and 0.0% ($n=448$), respectively in 1982. Relatively high proportions of dead stems were encountered only in dense stands of Tamarix (38.6% to 44.0%, $n=3$ stands), Salix exigua (0.94% to 27.4%, mean=7.4% for 6 stands), and Tessaria (50.8%, $n=1$), where dead stems were retained for long periods of time (Appendix 3.2). No dead Baccharis salicifolia or B. emoryi were seen along the river prior to 1983.

Flood-induced Plant Mortality

The percent mortality due to removal, drowning, and total estimated mortality of each common riparian plant species are presented in Table 3.2. Data from eddy and straight reaches in Zones A and B were pooled to produce this table, because most of the post-dam riparian corridor vegetation occurs in those settings. Estimates of total mortality are based on combined removal and drowning mortalities. Where removal data were not available (i.e. for less common species), removal was considered to be 0; therefore, the total mortality estimates are conservative.

Removal by Scouring

Removal data were compiled from several sources and are presented in Appendix 3.2. These data provided several independent estimates of removal for the more common species, and estimates of removal were averaged between techniques to obtain the mean total percent removal for each species (Table 3.2).

Levels of removal by scouring were significant for most species ($p<0.005$ and $df=1$); however, numbers of Salix gooddingii, Prosopis, and Acacia were not statistically different before and after 1983 (Table 3.2). Susceptibility to removal varied greatly between species. Removal varied from relatively low levels (0-20%) for species with deep tap roots, such as S. gooddingii, Acacia, Prosopis, and Tamarix, to higher levels of removal (20-79%) among shallow-rooted species, such as Baccharis spp. (and undoubtedly Aplopappus acradenius, Brickellia longifolia, and Gutierrezia spp. although data are lacking for these latter species). The highest levels of stem removal (68-100%) were found among shallow-rooted, clonal species, such as S. exigua, Tessaria,

Phragmites, Typha, Scirpus, and probably Aster spinosus. While levels of ramet (individual stem) removal were extreme for these species, clonal survivorship was quite high, except for macrophytic Typha and Scirpus. Genet (total clone) mortality levels ranged from 6.8% for Salix exigua to 31.4% for Phragmites. In contrast, clonal macrophytes, such as Scirpus and Typha, that occupied the river's edge prior to 1983, suffered removal rates of 88.9% to 100%, respectively. A gradient of survivorship by habitat preference was observed among clonal species, with macrophytes such as Typha, Scirpus and Phragmites subject to higher genet mortality than S. exigua at intermediate distances from the pre-1983 high water line, and highest survivorship among Tessaria clones which occupied Zones C and D away from the river.

Removal data for Tamarix indicate that a significantly greater proportion of scouring occurred in Zone A ($p < 0.005$, $df=2$). Because Tamarix is extremely well anchored, the trend of higher levels of removal near the river is probably valid for the other plant species as well. Overall removal rates of Tamarix were highest in cobble substrates, especially on cobble islands (exceeding 50%). Lower levels of removal (21.0%) were found in sand substrates and lowest rates occurred in boulder and bedrock settings (15.9%). Cobble islands appear to be highly disturbed substrates by flooding events. Sand is also readily eroded, but finer, underlying silt beds provide these deep-rooted plants with a better anchor, and boulder substrates do likewise (Gary 1963).

Prior to 1983, many large riverside beaches in eddy settings in this system were occupied by S. exigua, Tessaria, Tamarix and/or Baccharis, other perennials, herbs, and grasses. All plants on 12 of 15 such beaches were scoured away, and one of the three remaining beaches was left with only one Salix stem. The two remaining beaches lay on the inside of river meanders and were somewhat protected from substrate erosion. Excavations on four of five previously vegetated beaches revealed no root structure to at least 1.5m depth; and significant changes in sediment texture and stratification (Chapter 2) indicate that beach surface sediments were scoured away and then totally replaced during the subsidence of high flows. In several cases, the morphology of beaches redeposited by subsiding floodwaters was remarkably similar to that prior to the flood.

Lastly, the direction of the current at a given site may contribute to removal mortality. Anomalously high removal was observed at several locations, especially islands at Miles 61.0R and 71.5; however, this factor could not be measured accurately in this study.

Mortality Due to Drowning and Thrashing

Drowning coupled with thrashing was an important source of mortality of riparian plants subjected to prolonged flows in this system. Results gathered from quadrats in 1984 are presented in Appendix 3.1, and are summarized in Table 3.1. On average nearly 40% of all plants remaining in Zones A and B after flooding in 1983 had drowned (Table 3.2); however, rates of mortality due to drowning varied significantly between species ($p < 0.001$, $df=13,737$). All species except Acacia, S. exigua genets, and Tessaria genets showed a significant decrease in density due

to drowning ($p < 0.005$, $df=1$ for each species). Acacia (20.0% mortality), Tamarix (28.0%), and several other riparian species were relatively tolerant of inundation, while Prosopis (49.8%), Baccharis spp. (64.0% to 79.3%), Aplopappus acradenioides (83.2%) and Brickellia (62.0%) were intolerant of inundation stress. Three of the four species with deep tap roots suffered relatively low levels of drowning mortality (Table 3.2). Nearly all xeric-adapted species that had colonized post-dam beaches from the surrounding desert were intolerant of flooding. Desert Compositae, such as Dyssodia pentachaeta, Gutierrezia sarothrae, G. microcarpa, Aplopappus spinosus, Encelia farinosa, and Peucephyllum schottii suffered moderate to high levels of drowning mortality, as did Ephedra spp., Larrea and various cacti species.

Another flood-related impact in this system arose from covering of inundated plants with the aquatic alga, Cladophora. Following subsidence of high discharges in 1983 and 1984 Tamarix and other streamside plants were commonly found entirely coated with Cladophora, especially in Zone A. This "covering effect" was most pronounced from Glen Canyon Dam through Marble Canyon, but inundated plants and especially seedlings were found coated with Cladophora throughout the river corridor. The coating of drift algae dried and hardened, persisted for weeks to months, and may reduce or inhibit photosynthesis on affected plants.

Several remarkable cases of inundation tolerance were noted in this study. An examination was made of a cobble bar above the mouth of Parashant Canyon (Mile 198.5R) in mid-November, 1985, which contained several hundred dead Tamarix stems. Below the 570m³/sec stage 36 3m-tall Tamarix plants were observed with a small amount of regrowth foliage. While virtually all individual Tamarix growing in lower Zone A had perished from drowning or removal, these individuals had survived continuous submergence of their root crowns for more than 500 consecutive days and nearly continuous submergence for almost 850 days--far longer than Warren and Turner's (1975) reported maximum survival period for inundated Tamarix chinensis. Those authors reported that Tamarix growing in aggradational silt beds at the head of reservoirs could survive inundation for up to 90 days. The much longer period of inundation tolerance observed in this study may be attributed to 1) cold water temperatures which slow cellular metabolic rates; 2) highly oxygenated water, allowing for adequate respiration; and 3) clear water which may permit photosynthesis to continue despite inundation. The root zone may have provided an adequate source of CO₂ for these submerged riverside Tamarix.

Several mesic species also deserve mention with regard to their tolerance of prolonged inundation. A small clone of the yellow variety of Mimulus cardinalis grows at approximately the 1,130m³/sec discharge stage at Vasey's Paradise (Mile 31.0R). This plant managed to persist through prolonged inundation for three consecutive years. To our knowledge, this is the only individual of this race and our observations in 1985 indicate that it is apparently sterile because it produced no viable seeds. This unique plant lies in a precariously high impact setting, and yet has managed to persist. Crimson Mimulus and Adiantum

are common mesic species, and have proven to be tolerant of prolonged inundation.

The mesic sedge, Carex near scirpoidea var. curatorium, was observed growing below the 600m³/sec stage along the river during the drawdown in October, 1984. This species was found growing in dense beds at several sites in Marble Canyon and was cloning vigorously. At that time the clones had been fully submerged for nearly 1.5 years and were proliferating despite inundation. Clear, as opposed to turbid, water may allow such facultative macrophytes and highly inundation tolerant Tamarix to continue to photosynthesize even when fully submerged.

Mortality due to Burial

Tamarix growth at Mile 205.0L was vigorous but highly variable. Plants that had been buried by sand grew an average of 49.2cm in one year (n=12, SD=47.87), while non-buried plants grew 50.8cm/yr (n=21, SD=49.23). Growth rates were not statistically significantly different between buried and non-buried plants at this site (p>0.90, df=1,31).

In an experiment in 1982 Stevens assessed the responses of Tamarix and Salix exigua stems less than 3 years in age to simulated burial and excavation at Mile 43.1L. On August 11 the root crowns of 20 Tamarix and 20 Salix stems were exposed by excavation to a depth of 30cm to simulate erosional exposure. Twenty other root crowns of each species were covered with 30cm of sand to simulate burial. On October 16, 1982, experimental plants were reexamined. Of the plants which could be relocated, 5.3% (n=19) of the Tamarix and 5.6% of the Salix had succumbed to burial. Interestingly, 43.8% (n=16) of the Tamarix succumbed to exposure, while only 11.8% (n=17) of the Salix died. This pattern of higher mortality among Tamarix due to exposure, and higher overall mortality due to both causes combined, was observed following flooding in this system in 1984 and 1985.

While mortality resulting from burial could not be clearly distinguished from drowning, it was clear that non-clonal species were far more susceptible to this form of mortality than were clonal species. Tamarix were the most resistant non-clonal species and those that had been buried under redeposited sediments in 1983 survived a year or more if even a small portion of their canopy remained exposed to sunlight. This was observed at Mile 23.0L, 48.4R, 64.8R, 66.4L, 136.5L, 136.7L, 175.0R, 205.0L, and elsewhere; however, plants at 2 sites (136.7L and 175.0R) succumbed to burial in 1985. All four Baccharis species appeared uniformly stressed by burial, and nearly all Baccharis that had been covered to more than half their height by redeposited sediments were dead in 1984. Other plants that grow in clumps, such as Prosopis, Acacia, Brickellia, and xeric adapted Encelia and Gutierrezia showed similar negative responses to burial.

Clonal species showed a vigorous growth response to burial. In all cases observed, Salix exigua responded to burial with rapid colonization of newly deposited sediment beds. This was observed at miles 2.2L, 31.6R, 37.3L, 41.4R, 44.6L, 50.2R, 51.2L, 51.3L, 51.7LR (x2), 61.3L, 64.9R, 71.2R, 76.7L, 98.1R, 120.0R, 122.1R, and 142.5R. At Mile 122.1R, S. exigua stems that had been entirely buried under 2m of new sand for a

full year and then re-exposed by erosion, quickly produced new leaves and recovered. In 1985 it was observed that S. exigua dominated much of the heavily vegetated portions of the river bank from Mile 41 to Mile 70 where Tamarix had previously existed. This same response of vigorous growth following burial was observed for Tessaria throughout the river corridor, including sites at miles 40.9R, 43.5L, 43.6L, 67.5R, 131.9R, 164.5R, 173.0R, 185.5R, 186.0L, 207.7L, 207.9L and elsewhere. Where Phragmites australis, Equisetum spp. and Alhagi camelorum persisted, they too showed a vigorous regrowth response to burial. Lastly, Aster spinosus showed extremely vigorous regrowth following burial: a 15m x 30m quadrat of new sand at Mile 139.0R was almost entirely covered by spiny aster by June, 1984, and this species was recolonizing vigorously in most quadrats censused in 1984 and 1985.

Factors Influencing Mortality due to Drowning

The influence of plant height, distance from Glen Canyon Dam, reach type, substrate type, and floodzone (period of inundation) on levels of mortality due to drowning are presented in Figures 3.2A to 3.2E. Floodstage was most strongly and significantly correlated with mortality due to drowning ($p < 0.001$, $df = 2,748$). A total of 49.4% of all plants remaining in Zone A drowned, 26.2% drowned in Zone B, and 17.7% drowned in Zone C (Figure 3.2B). Data for Tamarix by itself also showed that mortality attributed to drowning was strongly correlated with floodstage ($p < 0.005$, $df = 2,168$). While some mortality of remaining stems must be attributed to battering and stripping of cambial layers, especially on submerged cobble bars, a large proportion of the mortality occurred in relatively quiet reaches where drowning is undoubtedly the primary source of mortality of the remaining plants.

Drowning mortality varied significantly between the five substrate types ($p < 0.01$, $df = 3,747$), with lowest mortality on bedrock substrates (23.2%), moderate mortality in silt, sand, and sand-cobble mixed substrates (30.6% to 31.2%), and highest mortality on cobble substrates (53.8%), as illustrated in Figure 3.2C.

Two-way analysis of variance of the mortality due to drowning of all species was conducted for floodstage and substrate types. This analysis showed the highest level of mortality (68.4%) occurred in cobble substrates in Zone A. This trend is further corroborated with data from cobble islands near miles 53 and 73, which had mean removal rates of 52.3% for Tamarix and 93.7% mortality of remaining stems.

Reach types (eddy, straight, riffle or rapid reaches) are measures of relative current velocity and reach type was shown to significantly increase drowning mortality (Figure 3.2A). Reach type is intercorrelated with substrate type in this system. For example, sand or cobble substrates occur in eddy or riffle reaches, respectively. Two-way analysis of variance using substrate type and reach type showed that drowning mortality decreased in sand substrates as current velocity increased, but mortality increased with velocity in cobble substrates.

Other factors which may influence plant mortality include distance from Glen Canyon Dam, plant height, and stem density. No significant relationship between river section and drowning mortality could be

discerned from data with all floodzones pooled (Figure 3.2E). Narrow reaches with little talus slope development are found in several reaches and seem to have sustained extreme levels of mortality. In such reaches from Miles 12 to 30 and Miles 144 to 164 little if any riparian vegetation survived below the $1,100\text{m}^3/\text{sec}$ discharge stage. Analysis of variance showed that drowning mortality was negatively correlated with Tamarix plant height ($R^2=0.236$, $p<.001$, $df=9,220$). The percent variation in Tamarix mortality explained by reach type, floodstage, substrate, stem density, and distance from Glen Canyon Dam was greatest in plants 3m or more in height ($R^2=41.2\%$, $p<0.004$, $df=8,40$) and R^2 values decreased progressively as lower height classes were included in the analysis. Stem density, a factor that may reduce removal mortality, was not shown to significantly influence rates of drowning.

Plant Growth and Flooding

Growth was measured on Tamarix growing in the 3 floodzones at mile 54.0R in June of 1984 and 1985. Thirty stems were marked on 10 plants growing in Zone A, Zone B, and Zone D in June, 1984 and these stems were remeasured in June, 1985. This analysis reiterated Stevens' (1985) findings that shoot mortality is extremely high in Tamarix as, on average, shoots marked in 1984 lost 12.4cm of stem length in all three zones. Zone A stems lost an average of 19.7cm of shoot ($n=18$) and Zone D plants lost an average of 15.0cm of shoot ($n=29$), while Zone B plants lost only an average of 6.1cm growth/shoot. Duncan's multiple range test showed that losses of shoot growth were not significantly different between zones. These losses were attributed to unexplained causes in Zone B and D, and to flood-related mechanical damage in Zone A.

In contrast, growth rates of Salix exigua stems at Mile 64.8 showed a mean stem increase of 99.2cm/stem ($n=17$, $SE=39.29$). Many of the marked willow stems were removed by beavers, limiting our final sample size. Differences between male and female growth rates were nonsignificant at this site.

Effects of Continued Flooding in 1984 and 1985

Prolonged, above average discharges were released in this system in 1984 and 1985, and the effects of continued flooding on adult plants and germination success were of interest in this study. Based on quadrat data for all species and height classes above 1.0m in 1984 and 1985, numbers of damaged and dead adult plants rose slightly in 1985, while numbers of all live plants increased dramatically in 1985 (Figures 3.3A and B). This increase was due to recruitment of 1984 seedlings which entered the greater-than-1.0m height class in 1985. The same pattern was observed in Tamarix alone in 1985, a species that dominates the riparian flora. Total numbers of seedlings nearly doubled on 12 quadrats between 1984 and 1985 (Figure 3.3C and D). In sum, these results suggest that flooding in 1984 and 1985 continued to damage and/or kill remaining adult plants, but that germination and establishment has been successful in the riparian corridor.

Colonization

Flooding is believed to promote germination and colonization of riparian plant species in this system (Hayden unpublished 1976). Following

flooding in 1980, mean seedling densities of mixed species reached $2,921/m^2$ on six $1.0m^2$ plots on previously uncolonized beaches. In September of 1983 dense beds of Tamarix seedlings were observed beneath the canopies of both Tamarix study sites that had been inundated by floodwaters. This was the first colonization event observed at these sites in 5 years. Seedling densities ranged from $4.5/m^2$ to $330/m^2$, with the higher germination taking place on a thin silt bed that had been deposited by tributary flooding. No Tamarix seedlings have ever been observed to germinate beneath the canopy of the Tamarix study site that was not inundated in 1983.

Analysis of quadrat data revealed that levels of colonization varied significantly between terrestrial plant species (Table 3.2). Tamarix seedlings were 5 times more abundant than seedlings of any other species in 1984. At a mean density of $0.003/m^2$, Acacia seedlings were three times as abundant as Prosopis seedlings and, as both have relatively high survivorship, Acacia may become a more conspicuous element of the new riparian vegetation. All clonal plant species produced a vigorous growth of new shoots. Rapid invasion of new beach deposits was observed among S. exigua, Tessaria, Phragmites, Alhagi, and Aster spinosus. Gutierrezia spp. and Dyssodia seedlings were the only talus slope species to re-colonize the post-flood beaches in abundance, and Encelia farinosa seedlings were common. Agave utahensis seedling densities were significantly higher in Floodzone B than in other zones at some sites in Marble Canyon, and this species demonstrated a rapid and extensive colonization response to flooding. No seedling Ephedra spp. were encountered, and this species was relatively common prior to 1983 in Zone B. Recruitment may compensate for the loss of adult plants in some of these species.

Colonization of newly deposited beaches by annual and herbaceous plants was observed in 1984 and 1985. The most common species on new beaches was the annual composite, Dicortia. Chorispermum nitidum, a chenopodiaceous species was rare in this system prior to 1983. In September of 1983 it was observed throughout the river corridor, and was evidently distributed by flooding. Polypogon monspeliensis and Distichlis spicata, both halophilic grasses, have become more abundant throughout the river corridor, while densities of other grasses (e.g. Sporobolus giganteus, Muhlenbergia spp. and Bromus marginatus) appear to have been reduced. The submergent macrophyte, Elodea sp., was observed growing in dense beds in upper Marble Canyon in October, 1985. Prior to 1983 this species was rare along the river but now appears to be well-established in the niche formerly dominated by Cladophora. A list of the common plants of the riparian corridor observed during this study is provided in Appendix 3.3.

Light Intensity

Light intensity was significantly greater beneath flood-damaged stands of both Salix exigua and Tamarix as compared to undamaged stands of these two plant species ($p < 0.001$, $df = 1,68$). Flood-damaged Salix stands admitted an average of 52.2% of the ambient light while undamaged stands admitted only 11.7% of the ambient light ($p < 0.001$, $df = 1,22$). Damaged Tamarix stands admitted 33.6% of the ambient light and undamaged Tamarix stands admitted only 6.3% of the ambient light.

Significantly more ambient light reached the ground surface beneath Salix stands than beneath Tamarix stands ($p = 0.024$, $df = 1,68$). Insolation affects substrate temperature and drying rate, and may thereby affect seedling success.

Changes in Diversity and Community Structure

Changes in species diversity were estimated using Shannon-Weaver H' index of diversity for pre-1983 and post-1983 stem counts on 24 quadrats. Table 3.3 shows a slight but highly significant overall decline in species diversity in this system as a result of flooding. H' decreased from 0.478 ($n = 24$, $SE = 0.033$) before 1983 to 0.445 ($n = 24$, $SE = 0.034$) in 1984 ($p = 0.004$, $df = 23$). Oneway analysis of variance with Duncan's multiple range test for H' by reach type showed similar but nonsignificant trends in difference between reach types before 1983 and in 1984. Both before and after 1984, diversity was lowest in eddy reaches, intermediate in straight and rapid reaches, and highest in riffle settings. Nonsignificant trends in these data suggest a pattern of dominance by fewer species on beaches, and higher diversity in the more ecologically disturbed cobble bar/riffle settings.

Change from estimated pre-flood to post-flood plant community structure was evaluated using J' , an index of the evenness of species distributions. Evenness decreased slightly but significantly after flooding in this system (Table 3.3). Mean pre-flood evenness ($J' = 0.560$, $SE = 0.036$) was significantly higher than post-flood evenness ($J' = 0.517$, $SD = 0.033$) at $p = 0.006$ ($df = 23$). Student's t -test analyses of changes in J' by reach type showed that evenness in straight and riffle reaches declined significantly after flooding ($p = 0.037$ and 0.044 , respectively; $df = 5$), while J' values did not vary significantly between years in eddy and rapid reaches. These results indicate that differential flood-induced mortality changed the riparian plant community structure slightly but significantly in this system. Differential, flood-induced recruitment is likely to exert further changes on community structure in this system, and those changes are currently under study by one of us (Waring).

Discussion

The effects of flooding on riparian vegetation in this system were complex. High discharges killed more than 50% of the riparian plants below the $1,700\text{m}^3/\text{sec}$ stage by direct removal, drowning and/or burial. Virtually all riparian plant species along the Colorado River in Grand Canyon were highly susceptible to flooding stress; however, mortality rates varied greatly between species. Shallow-rooted Baccharis spp., Brickellia longifolia, and Aplopappus acradenius suffered higher levels of drowning mortality than did species with deep tap-roots, such as Salix gooddingii, Tamarix chinensis, Acacia greggii, and Prosopis glandulosa. Despite high levels of areal loss among several common clonal species (Phragmites communis, Salix exigua, and Tessaria sericea), ramets of most clones persisted, and overall clonal mortality rates were low. Xeric-adapted plant species, such as Ephedra spp., various cacti, Larrea tridentata, and Encelia farinosa, that had colonized riparian beaches from the surrounding desert were intolerant

of inundation and suffered high levels of mortality. Both species diversity and community structure (evenness) of the riparian plant community declined slightly but significantly as a result of flooding in 1983. Inundation did not result in a loss of plant species from this system, as far as we were able to determine, although Baccharis spp. and several species suffered extremely high levels of mortality in some reaches. The range of S. exigua apparently remained unchanged, with a few new clones observed in the lower Canyon.

The duration (period) and magnitude (discharge stage) of flooding were factors that most influenced plant mortality. Plants growing at lower discharge stages suffered the highest levels of removal and drowning due to a longer period of submergence in swifter, more turbulent currents. Plants presently occupying the riparian corridor in this system are shrub and small tree species that are adapted to withstand short periods of flooding, such as flashfloods. Both the Havasu Creek and lower Diamond Creek drainages were subject to exceptionally large (>ten-year interval) flashfloods in 1984, yet a high percentage of the riparian plants, especially Baccharis spp. and Brickellia, survived and quickly recovered from those floods, even though the tributary vegetation was subject to far greater turbulence than was the riverside vegetation during the 1983 flood. This observation suggests that mortality of some native species may be influenced more by the period of flooding than by the magnitude of flooding; however, this observation will require rigorous testing before it can be verified and used in management.

Flooding promoted increased germination of many riparian species, especially Tamarix, in 1984 and 1985. The structure of this plant community was altered by differential flood-induced mortality of adult plants, and the community will continue to change through time as seedlings established in 1984 and 1985 mature and come to dominance. Will Tamarix continue to dominate the riparian corridor, or will altered substrate conditions prevent successful establishment? It will also be interesting to see if Acacia becomes dominant over Prosopis through time, because Prosopis is presently firmly established on the pre-dam terraces. Flooding resulted in increased exposure of the substrate beneath stands of Tamarix and Salix exigua and this exposure may have two effects. Increased light may allow other plant species to invade these dense stands, which appear light limited (especially in the case of Tamarix). Increased light may also increase surface temperature and increase the desiccation rate of the substrate, thereby negatively affecting seedlings. Stevens (unpublished 1985) suggested that moderate shading of the substrate beneath S. exigua stands facilitated establishment of numerous understory species, while dense Tamarix stands exerted inhibitory effects on establishment of understory species.

Larger plants are generally more tolerant of flooding (Kozlowski 1984). For example, the few large Salix goodingii trees along the river had far higher survivorship than did Tamarix or other small tree species. Substrate changes, erosion, herbivory by beavers, and the difficulties of seedling establishment have promoted the proliferation of shrub and small tree species over larger native trees, such as Populus fremontii, Salix goodingii, and Fraxinus pennsylvanica in this system. Populus and Salix goodingii existed in the riparian zone prior

to 1963 (Turner and Karpiscak 1980) and could survive there now. With special efforts these species could be reintroduced; otherwise, this system may continue to be dominated by fast-growing shrubs which, by their small size, are more susceptible to flood-induced removal and drowning. A cottonwood and willow planting program could be conducted inexpensively in the Grand Canyon using volunteer labor, and would make a major contribution to avian species diversity and recreational quality in this system.

Several other ecological trends bear consideration in the appropriate management of this system. When a normal flow regime has been established, riparian vegetation will colonize the edge of the normal discharge stage. Riparian vegetation will become increasingly profuse until it is once again disturbed. Long-term stability of discharges would encourage development of the riparian plant community, while erratic high releases, such as occurred in 1983, retard or reduce plant community development.

While extreme flooding is detrimental to this system, a rare, low-magnitude, short-duration flood will promote seedling establishment. Riparian plant communities in this system have, in the past, tended to develop as monospecific stands, for as yet undetermined reasons. Seedling establishment is brought about by flooding and the timing of flooding could be used to selectively deter establishment by exotic species and simultaneously increase the establishment of native species. For example, Tamarix flowers heavily from April through June, and its seeds last only a few weeks in the wild (Horton et al. 1960; Stevens unpublished 1985). In contrast, native plant species, including Salix spp., Prosopis, Acacia, and Baccharis spp. commonly set seed from July through September. By delaying flooding until July or August, Tamarix germination could be reduced and germination by native species could be facilitated. To promote seedling establishment, rare, above-normal floods in this system need not exceed approximately 1,200m³/sec, need not last more than approximately two weeks, and may need to be repeated two consecutive years out of, for example, every seven to ten years, to be determined by ongoing studies of this system.

Continued disruption by flooding has had a significant impact on the Colorado River corridor in Grand Canyon. The development of dense riparian vegetation is to be expected downstream from large impoundments and, while not natural, these anthropogenic riparian ecosystems are of considerable biological and recreational value. The fate of post-dam riparian zone vegetation in Grand Canyon now lies wholly in the hands of the Bureau of Reclamation and the National Park Service. Responsibility for appropriate and intentional management must be quickly assumed in order to preserve and extend the life of this ecosystem.

Conclusions

The following conclusions are drawn from this portion of the study:

1. Record post-dam flooding in 1983 in the Colorado River corridor downstream from Glen Canyon Dam constituted a significant disturbance to the riparian ecosystem, reducing the total number of individual riparian plants in Zones A and B by more than 50%. Sources of mortality included removal by scouring, drowning, and burial under redeposited fluvial sediments.
2. Various species of riparian plants responded differently to this disturbance event, depending on plant architecture, inundation tolerance, and burial tolerance:
 - a) Tree-forming species with deep tap roots (e.g. Salix goodingii, Prosopis, Acacia, and Tamarix) were more resistant to removal by scouring, as compared to clonal species (e.g. Salix exigua and Tessaria sericea) or other shallow-rooted species (Baccharis, Aplopappus, Brickellia, etc.).
 - b) Drowning accounted for nearly 40% of the observed mortality. Salix, Acacia, Tamarix, and Tessaria were relatively resistant to inundation, while Prosopis, Baccharis, Brickellia, Aplopappus, and xeric-adapted species were ill adapted to inundation stress.
 - c) Species tolerant of burial included Tamarix and clonal Equisetum, Phragmites, Salix, Alhagi, Aster, and Tessaria, while those intolerant of burial included species which grew as clumps (Prosopis, Acacia, Baccharis, Brickellia) and xeric-adapted species).
3. Plant mortality was strongly correlated with proximity to the river (stage), with more than 49% mortality in Zone A, 26% mortality in Zone B and nearly 18% mortality in Zone C.
4. Plant mortality varied according to substrate type. Mortality was highest on cobble substrates, moderate on sand and mixed sand-cobble substrates, and lowest on bedrock. Mortality was also positively correlated with current velocity.
5. Both Salix and Tamarix were capable of rapid regrowth, but Salix grew faster than Tamarix in some settings.
6. Post-flooding clonal reproduction in Salix exigua and Tessaria was vigorous and these species rapidly colonized new beach sediments in several reaches. Sexually reproducing Tamarix and other species have been slower to recolonize habitat lost through flooding disturbance.
7. Community diversity and structure (evenness) declined slightly but significantly due to the disproportionately great reduction in Baccharis densities as a result of flooding in 1983. Apparently no plant species were lost from the river corridor because of the flooding event.
8. Flooding stimulated germination in this system and exposed the substrate beneath stands of Tamarix and S. exigua to higher levels of insolation. Flooding in 1983 and subsequently resulted in widespread

germination of several riparian plant species, particularly Tamarix and, to a lesser extent, Baccharis and Brickellia. Seedlings of common clonal species, such as Salix exigua and Tessaria, were not found.

9. Careful management of discharge might be used to shift the dominance of Tamarix in this system in favor of native plant species.

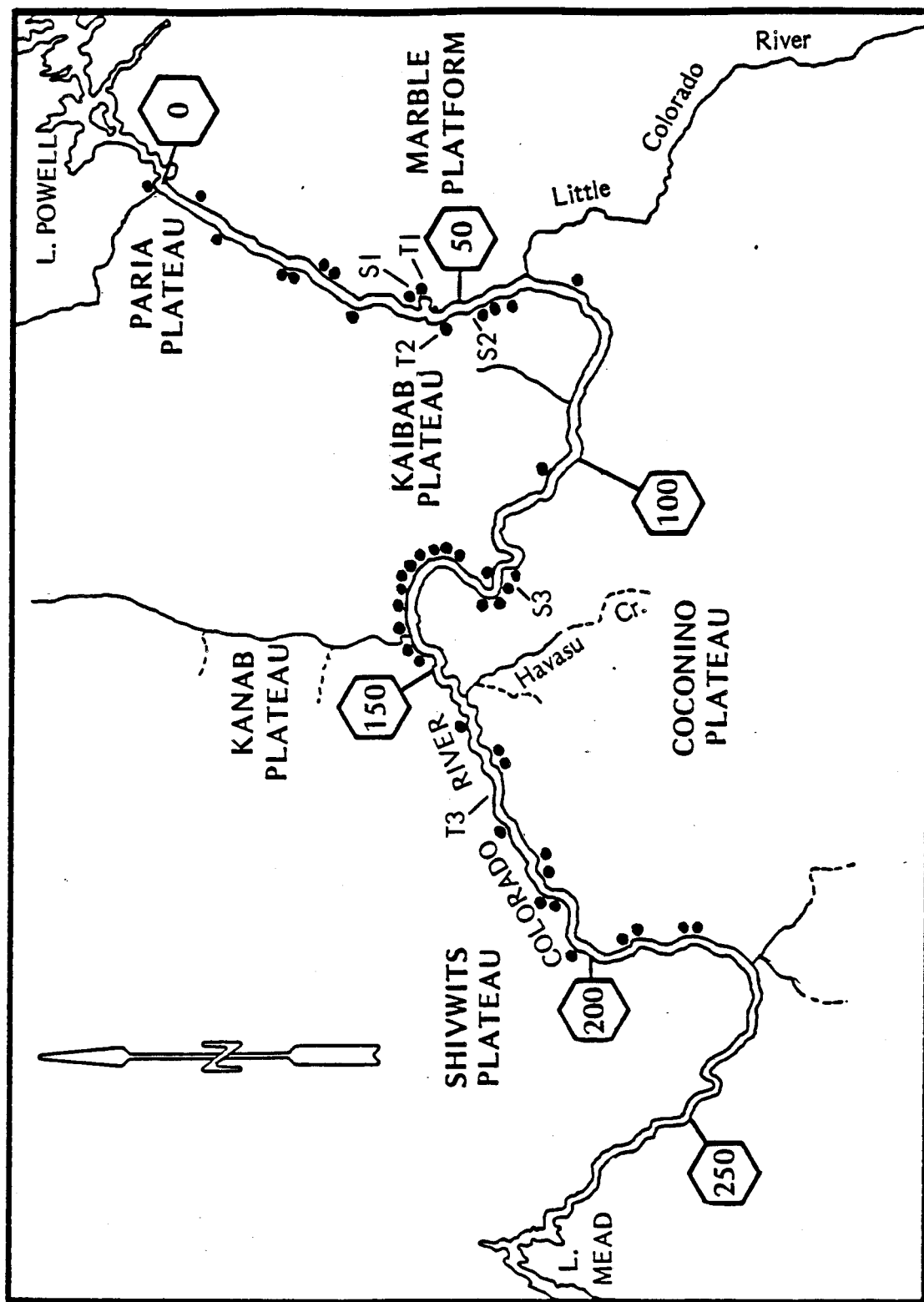


FIGURE 3.1: QUADRAT AND 10m x 30m SALIX AND TAMARIX STUDY SITES USED TO ASSESS THE EFFECTS OF 1984 FLOODING ON RIPARIAN PLANTS. TAMARIX = T, SALIX = S.

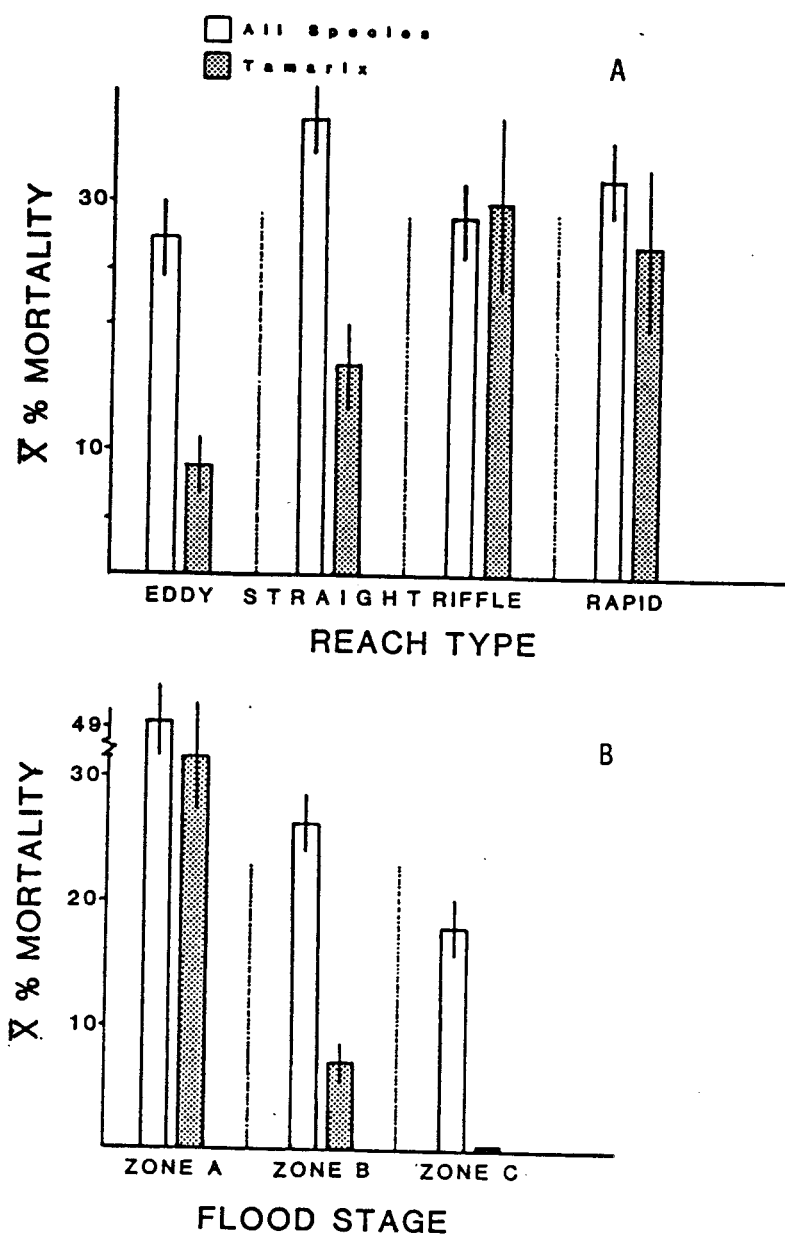


FIGURE 3.2A: PERCENT MORTALITY OF ALL RIPARIAN PLANT SPECIES AND TAMARIX BY REACH TYPE. SEE TEXT FOR STATISTICS.

B: PERCENT MORTALITY OF ALL RIPARIAN PLANT SPECIES AND TAMARIX BY FLOODSTAGE. SEE TEXT FOR STATISTICS.

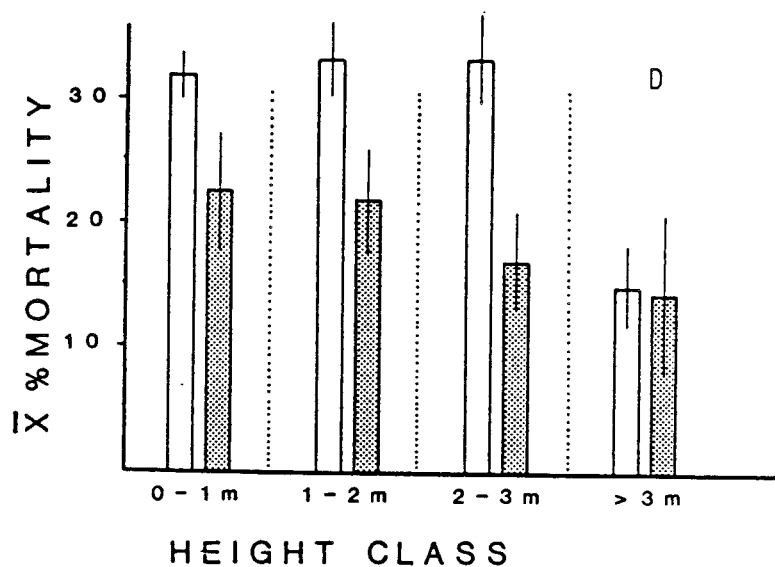
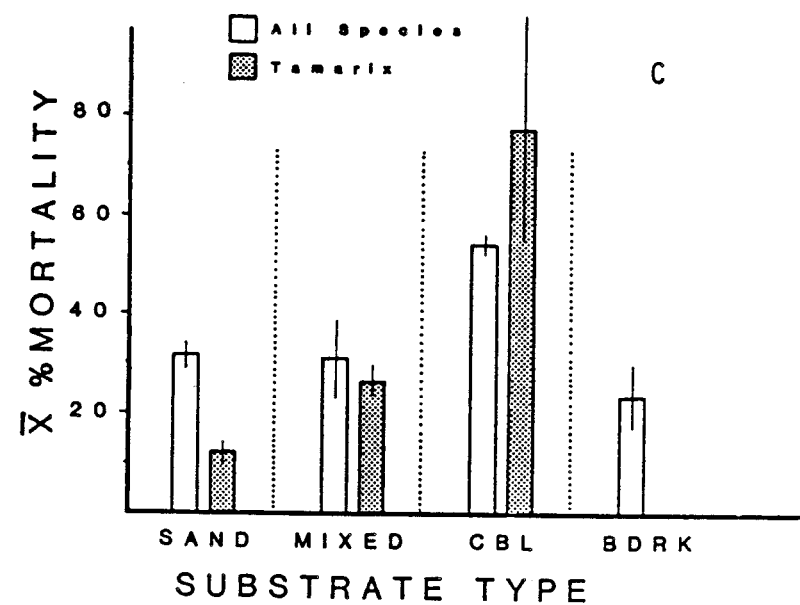


FIGURE 3.2 C: PERCENT MORTALITY OF ALL RIPARIAN PLANT SPECIES AND TAMARIX BY SUBSTRATE TYPE. SEE TEXT FOR STATISTICS.

D: PERCENT MORTALITY OF ALL RIPARIAN PLANT SPECIES AND TAMARIX BY HEIGHT CLASS. SEE TEXT FOR STATISTICS.

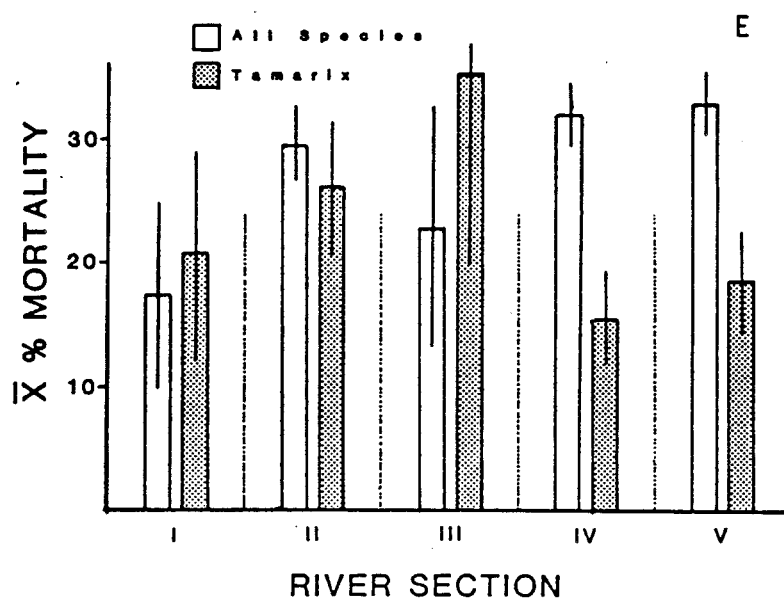


FIGURE 3.2E: PERCENT MORTALITY OF ALL RIPARIAN PLANT SPECIES AND TAMARIX BY RIVER SECTION. SEE TEXT FOR STATISTICS.

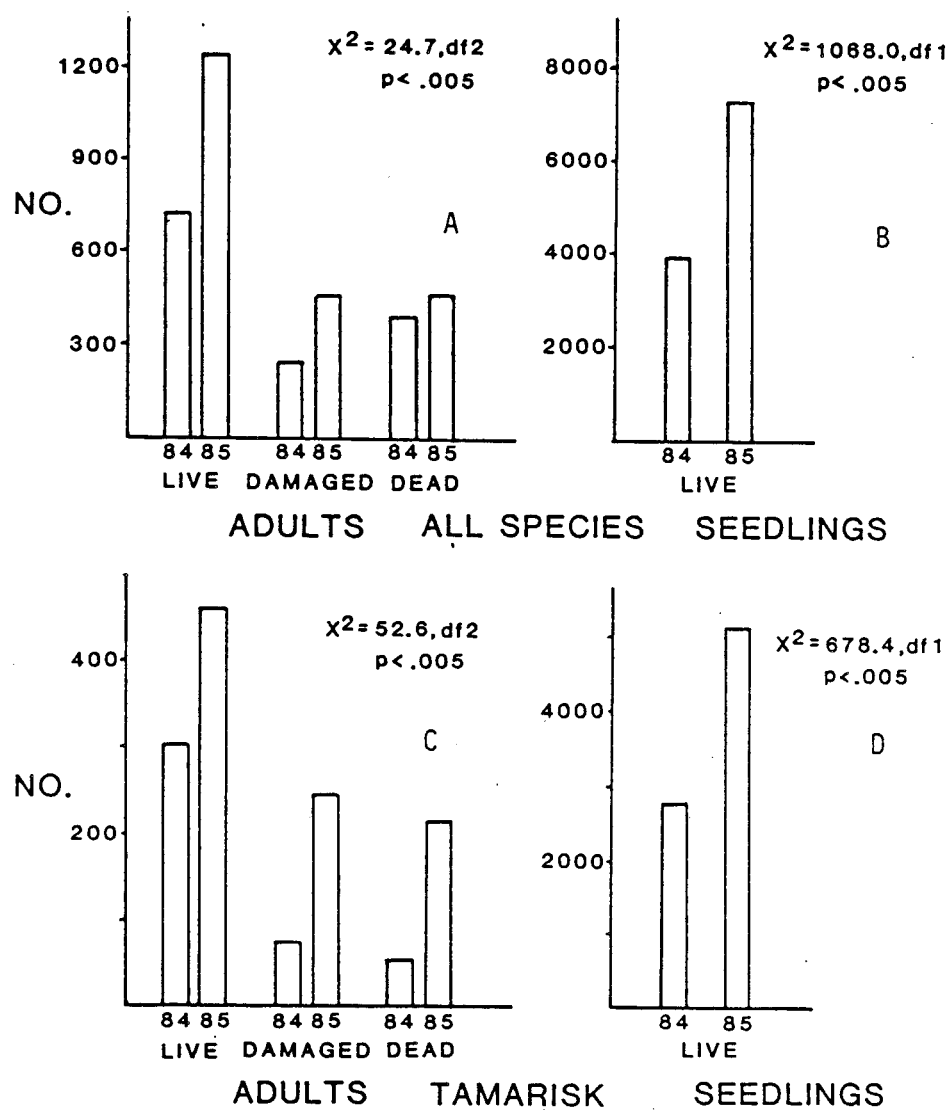


FIGURE 3.3A & B: COMPARISON OF CONDITION (LIVE, DAMAGED, DEAD) OF ALL ADULT PLANT (A) AND ALL SEEDLING (B) SPECIES IN 1984 AND 1985.

FIGURE 3.3C & D: COMPARISON OF CONDITION OF ADULT (C) AND SEEDLING (D) TAMARISK IN 1984 AND 1985.

TABLE 3.1 : SUMMARY OF APPENDIX 3.1 : QUADRAT DATA
ON DROWNING MORTALITY BY PLANT SPECIES

SPECIES	MEAN %DROWNED IN ZONE A	MEAN %DROWNED IN ZONE B	MEAN %DROWNED IN ZONE C	MEAN TOTAL % DROWNED
Tach	31.69	6.98	0.00	19.74
frequency =	95	72	11	178
Saex	21.36	10.65	33.33	17.06
frequency	20	21	3	44
Tese	86.13	10.79	9.06	28.84
frequency	15	29	17	61
Basp	68.84	33.10	27.50	53.11
frequency	41	22	8	71
Basr	79.33	59.33	23.15	59.77
frequency	23	24	12	59
Basg	100.00	25.14	3.13	24.04
frequency	1	7	4	12
Prgl	79.17	29.90	0.00	36.46
frequency	12	17	11	40
Acgr	0.00	12.50	0.00	5.97
frequency	1	21	22	44
Brln	70.50	61.67	32.63	56.00
frequency	10	21	13	44
Haac	100.00	76.74	23.86	47.86
frequency	1	9	13	23
Assp	18.79	19.09	22.81	20.36
frequency	11	27	21	59
Gusp	25.63	42.04	29.20	33.74
frequency	6	19	24	49
Other Riparian Species	31.11	0.61	25.00	18.47
Other Talus Spp.	100.0	36.24	21.69	32.99
frequency	3	25	25	53
TOTAL %DROWNED	49.37	26.17	17.66	29.23
frequency	244	319	188	751

TABLE 3.2: PERCENT REMOVAL, PERCENT OF REMAINING PLANTS DROWNED, ESTIMATED TOTAL PERCENT MORTALITY, AND SEEDLING DENSITY/M² OF COMMON PERENNIAL PLANT SPECIES IN THE COLORADO RIVER RIPARIAN CORRIDOR IN GRAND CANYON, 1984. DATA POOLED FOR ZONES A AND B IN STRAIGHT AND EDDY REACHES.

SPECIES	MEAN PERCENT REMOVAL	N	MEAN PERCENT DROWNED	N	ESTIMATED TOTAL PERCENT MORTALITY	MEAN SEEDLING DENSITY/M ²
DEEP TAP ROOTS						
<u>Tamarix chinensis</u>	19.32 **	4452	27.99 **	4584	41.90 **	0.491
<u>Prosopis glandulosa</u>	0.50 ns	108	44.79 **	303	45.06 **	0.001
<u>Acacia greggii</u>	9.09 ns	11	20.00 ns	39	27.27 ns	0.003
<u>Salix gooddingii</u>	0.00 ns	18	5.56 ns	18	5.56 ns	0.000
CLONAL, SHALLOW ROOTS						
<u>Salix exigua</u> (ramet)	72.42 **	12828	11.99 **	4922	75.72 **	0.002 s
<u>Salix exigua</u> (genet)	16.18 ns	68	0.00 ns	68	16.18 ns	---
<u>Tessaria sericea</u> (ramet)	90.60 **	271	44.02 **	4073	94.74 **	0.083 s
<u>Tessaria sericea</u> (genet)	9.13 ns	32	0.00 ns	32	9.13 ns	---
<u>Aster spinosus</u> (genet)	---	---	19.02 **	413	19.02 **	0.017
<u>Phragmites australis</u> (genet)	42.31 *	26	0.00 ns	26	42.31 **	0.000
<u>Typha latifolia</u> (genet)	83.33 **	12	0.00 ns	12	83.33 **	0.000
<u>Scirpus</u> sp. (genet)	100.00 ns	2	0.00 ns	2	100.00 ns	0.000
SHALLOW ROOTS						
<u>Baccharis salicifolia+emoryi</u>	74.56 **	510	63.98 **	731	90.84 **	0.008
<u>Baccharis sarothroides</u>	20.72 **	1004	70.28 **	1216	76.44 **	0.004
<u>Baccharis sergiloides</u>	---	---	79.34 **	30	79.34 **	0.000
<u>Brickellia longifolia</u>	---	---	62.04 **	43	62.04 **	0.015
<u>Aplopappus acracenius</u>	---	---	83.23 **	113	83.23 **	0.005
<u>Gutierrezia</u> spp.	---	---	35.39 **	416	35.39 **	0.006
<u>Encelia farinosa</u>	---	---	63.64 **	55	63.64 **	0.001
TOTAL MEAN	23.82 **	6243	38.95 **	8101	53.49 ** (14344)	0.636

TABLE 3.3: FLOOD-INDUCED CHANGES IN PLANT SPECIES DIVERSITY (H') AND EVENNESS (J') IN THE COLORADO RIVER CORRIDOR, GRAND CANYON. DATA POOLED FOR 24 INUNDATED SITES.

REACH TYPE	YEAR	DIVERSITY		EVENNESS	
		MEAN H' (N = 6)	P	MEAN J' (N = 6)	P
Eddy	Pre-1983	0.356		0.435	
	SE	0.060	NS	0.075	NS
	1984	0.326		0.401	
	SE	0.057		0.074	
Straight	Pre-1983	0.493		0.579	
	SE	0.077	0.026	0.073	0.037
	1984	0.420		0.480	
	SE	0.092		0.102	
Riffle	Pre-1983	0.592		0.654	
	SE	0.024	0.040	0.072	0.044
	1984	0.561		0.620	
	SE	0.022		0.062	
Rapid	Pre-1983	0.471		0.570	
	SE	0.067	NS	0.057	NS
	1984	0.472		0.569	
	SE	0.060		0.043	
TOTAL	Pre-1983	0.478 (n = 24)		0.560 (n = 24)	
	SE	0.033	0.004	0.033	0.006
	1984	0.445 (n = 24) (df = 23)		0.517 (df = 23)	
	SE	0.034		0.036	

**CHAPTER IV: EFFECTS OF FLOODING ON HERBIVOROUS INVERTEBRATE
POPULATIONS, WITH OBSERVATIONS ON TROPHIC RELATIONSHIPS
IN THE COLORADO RIVER RIPARIAN ECOSYSTEM IN GRAND CANYON**

Introduction

Regulation of the Colorado River's flow in Grand Canyon led to a dramatic increase in riparian vegetation (Turner and Karpiscak 1980), and to marked increases in avian and terrestrial vertebrate populations (Carothers and Aitchison 1976; Brown 1986 in press). Equally dramatic but less thoroughly appreciated have been post-dam increases in insect populations. Stevens (1976a) recorded the presence of several thousand terrestrial invertebrate species from the riparian corridor, in nearly 260 families of arthropods. He found the riparian invertebrate fauna in Grand Canyon to be dominated by terrestrial Diptera (Calliphoridae, Sarcophagidae, Tachinidae, etc.), adult forms of aquatic Diptera (especially Chironomidae), herbivorous insects (especially Cicadidae, Cicadellidae, Aphididae, Psyllidae, Miridae, other Heteroptera, Coleoptera, and Lepidoptera), ground-dwelling forms (Arachnida, Scorpionida, Collembola, and Coleoptera), and predatory Hymenoptera (especially Formicidae, Pompilidae, and Sphecidae). The ecological roles these taxa play in riparian trophic structure and ecosystem function has not been fully explored, although these invertebrates serve as pollinators, regulate populations of other invertebrates, and provide resources for many terrestrial and aquatic vertebrates. Invertebrates are difficult to sample and identify, and invertebrate population dynamics require intensive sampling over long periods of time. These constraints have limited the analysis of invertebrate dynamics in ecosystems research.

Stevens (1976b) made several observations on the ecology and trophic relationships of terrestrial invertebrates in the Colorado River riparian corridor in Grand Canyon. Post-dam terrestrial insect populations were far more diverse and abundant in the riparian zone than in the surrounding desert environment. Exotic plant species, such as Tamarix, Melilotus and Alhagi, supported a density and biomass of insect life equal to or higher than that found on native plant species, particularly while these species were blooming. With the exception of chironomid midges and simuliid gnats, which were abundant, few insect taxa occupied the Colorado River itself.

In 1985 Stevens (unpublished) reported on the population dynamics of phytophagous invertebrates associated with Tamarix chinensis and Salix exigua. In that study he found: (1) non-blooming Tamarix supported a low diversity of phytophagous insects, strongly dominated by Opsius stactogalus (Cicadellidae); (2) native S. exigua, which is rapidly expanding its range in this system (Brian unpublished 1982), supported a far greater diversity of phytophagous cicadellids, mirids, psyllids, aphids, and other phytophagous insects than did Tamarix; (3) despite the great difference in species richness on these two plant species, they supported an approximately equivalent biomass of phytophagous insects during "normal" discharge years; (4) both plant species were subject to outbreaks of phytophagous insects in 1980, a year characterized by

higher-than-normal flows; (5) the roots of both plant species were fed upon by the Apache cicada (Diceroprocta apache), but contrary to the findings of Glinski and Ohmart (1984), S. exigua shoots were preferred over Tamarix shoots as oviposition sites; and (6) beavers generally preferred S. exigua to Tamarix and occasionally harvested entire willow clones (beavers harvested Tamarix more frequently in the lower reaches of Grand Canyon). Furthermore, he suggested that invertebrate herbivory was not a mechanism of riparian plant succession in this system except perhaps during outbreak (flood) years when Opsius populations on Tamarix reached high levels. He noted that flooding in 1980 stimulated germination but that successful seedling establishment by Tamarix or S. exigua was extremely rare in this system, and thus any dispersal mechanism, such as herbivory by beavers, that favored one plant species over the other could lead to a successional replacement.

Objectives

In this study we examined the responses of invertebrate populations, especially those of chironomid midges and the cicadellid, Opsius stactogalus, to flooding in Grand Canyon. We asked the following questions:

1. Did flooding in 1983 affect phytophagous insect diversity on Tamarix chinensis or Salix exigua?
2. Did phytophagous insect community similarity change as a result of flooding?
3. Did the impact of flooding on invertebrate herbivore populations vary with distance from Glen Canyon Dam?
4. How do flood-induced changes in invertebrate populations such as cicadellids, cicadids and chironomid midges, affect higher trophic levels in this system?

Methods

To address the issue of how invertebrate populations responded to flooding we sampled several 10m x 30m Tamarix sites and Salix exigua sites studied by Stevens from 1980 to 1983 (Figure 3.1). These study sites were established in pure, even stands of vegetation and were undisturbed by river recreationists. Tamarix sites included 0.1R, T1 (Mile 43.5L), T2 (Mile 48.4R), Mile 143.2R, T3 (Mile 169.5R), and T4 (Mile 205.0L). T1 and T2 were moderately damaged by flooding from 1983 to 1985, while most of T3 lay above Zone B. Tamarix sites T1, T2, and T3 were sampled three times each in the summers of 1984 and 1985, with T1 and T2 also sampled in October, 1984. Other Tamarix sites were sampled only in August, 1984. The S. exigua sites used in this research included: Mile 1.2R; S1 (Mile 43.1R); S2 (the only one of Stevens' original six Salix exigua study sites that remained intact after 1983 and the site used in this study, Mile 50.2R); S3 (64.8R); S3.5 (122.2R); and 133.5R. The S2 site was sampled four times in 1984 and three times

in 1985, while the other Salix sites were sampled only in 1984. To address the effects of distance from Glen Canyon Dam on herbivorous insect populations, samples from 5 stands of Tamarix and 5 stands of S. exigua were compared in August, 1984.

Collection methods were those of Stevens (unpublished 1985). At each site fifty 2m sweeps were made in vegetation using a 30cm diameter cloth insect net. Invertebrates were sampled in full sunlight to maximize the sample size. Invertebrate samples were collected and killed using ethyl acetate and samples were returned to the laboratory for analysis. Specimens were identified to species, counted, and classified by guild as herbivores, predators, parasitoids, or incidentally-occurring species. Specimens were sent to the U. S. Department of Agriculture Insect Identification and Beneficial Insect Introduction Laboratory in Beltsville, Maryland for verification of identification.

Invertebrate data were compared and contrasted using t-tests and analyses of variance (Snedecor and Cochran, 1980). To compare patterns in phytophagous herbivore community structure and similarity before and after flooding on S. exigua and Tamarix we calculated Pielou's J' , as described in Chapter 3, and Stander's (1970) index of community similarity:

$$SIMI = \frac{\sum p_{ij}p_{in}}{(\sum p_{ij}^2)^{1/2}(\sum p_{in}^2)^{1/2}}$$

where p_{ij} and p_{in} are the proportions of species i in samples j and n , respectively. This statistic varies from 0 for entirely dissimilar communities to 1.0 for identical communities. It incorporates both species richness and evenness and is relatively independent of sample size (Sullivan 1975).

Observations on the trophic dynamics of fluvial and riparian components of this ecosystem were made in the field, and a general scheme of ecological interactions was developed from these observations.

Results

The present study added 10 new species to the list of phytophagous invertebrates associated with Tamarix in the United States, and identified for the first time 13 species of herbivores that feed on S. exigua. Appendix 4.2A and B provide a complete list of the invertebrate species collected from Salix in Grand Canyon, and from Tamarix in Grand Canyon and elsewhere in the United States (Stevens unpublished 1985). Such host records are important as phytophagous insect populations may reach outbreak proportions and their contribution to the resource base for higher trophic levels in this system may depend on the discharge regime. Appendix 4.1 lists the invertebrate collection data gathered during the course of this study, and is summarized in Figures 4.1 through 4.6.

Salix exigua Herbivores

The invertebrate herbivore fauna associated with Salix exigua consisted of numerous heteropteran species, especially cicadellids and mirids (Figure 4.1), and this willow species also supports a great diversity of parasitoid species. With a single exception, the herbivore community on S. exigua remained basically unchanged following flooding: elevated populations of the chrysomelid, Disonycha alternata (Illiger), were observed feeding on S. exigua throughout its range along the river in 1984 and 1985. Examination of exhaustive collecting data from S. exigua stands prior to 1983 (Stevens 1976, 1985) showed this leaf-feeding beetle was not present before flooding. Outbreak populations of Disonycha were also observed on vigorously growing stands of Aster spinosus in Marble Canyon in 1985.

Tamarix chinensis Herbivores

The invertebrate herbivore guild on Tamarix is depauperate and is dominated by Opsius stactogalus Fieber, a host-specific, exotic leafhopper (Liesner 1971; Watt et al. 1976; Stevens unpublished 1985; Table 4.2B). The small number of Tamarix herbivores may be attributable to the taxonomic novelty, anti-herbivore biochemistry, and the relatively short period of time Tamarix has been present in the system. Opsius populations reached outbreak proportions in 1980 and 1984, years of moderately high discharges (Figure 4.2A). Opsius populations peaked in mid- and late-summer following the subsidence of floodwaters in those years. In 1984 populations of an Opsius egg parasitoid believed to be Barypolynema saga Girault (Mymaridae) reached outbreak proportions as well. This egg parasitoid may exert some control over Opsius populations, but the extent of this control is not known. If Opsius are consumed by terrestrial vertebrates in this ecosystem their populations may provide a substantial food resource in years when resource availability is otherwise reduced by flooding.

In addition to Opsius stactogalus, other herbivores were found associated with Tamarix. The armored scale, Chionaspis etrusca Leonardi (Diaspididae) had been collected by Stevens (1985) from 1980 to 1982 at Mile 169.5R on Tamarix growing on pre-dam terraces. These plants appeared moisture stressed and supported few other herbivores. Chionaspis outbreaks occurred in 1981 and 1982 at this site, and populations of the scale-feeding coccinellid, Rhyzobius lophanthae (Blaisdell) also increased there. Chionaspis has been collected on Tamarix at numerous localities in the Southwest (McKenzie 1956; Liesner 1971) and is a European exotic, introduced along with its host as early as 1908. In 1984, Tamarix at Mile 139.0R were heavily infested with Chionaspis, and this was the furthest upstream we have observed this scale insect. The affected plants appeared stressed by burial under redeposited sediments. In August, 1985 much of that redeposited sediment bed had eroded away, perhaps alleviating conditions of moisture-stress there, and no sign of Chionaspis was found. Infestation of Tamarix by Chionaspis appears to be controlled by moisture stress.

Another scale-like herbivore on Tamarix was found on moisture-stressed plants at Lees Ferry, Arizona. The pseudococcid mealybug, Phenacoccus helianthi (Cockerell) is a generalist native to the Southwest (McKenzie, 1967). This species is rare on Grand Canyon Tamarix.

Relative Abundance of Invertebrate Herbivores

Patterns of invertebrate distribution on Tamarix and S. exigua remained similar after 1983 to those previously described by Stevens (unpublished 1985). The herbivore community on S. exigua was comprised of Empoasca, Idiocerus, Alconeura (Cicadellidae), mirids, psyllids and aphids, while that on Tamarix was dominated by Opsius stactogalus. Paired t-tests on a matched pair of study sites (T2 and S2) showed that mean herbivore abundance from August, 1982 through July, 1985 was 288.3 insects/50 sweeps on S. exigua and 289.5 insects/50 sweeps on Tamarix, not statistically different at $p = 0.755$ ($df = 7$). Stevens (op. cit.) found that abundance data from sweep-netting were highly correlated with actual biomass of herbivores/g photosynthetic material on these plant species. Figure 4.1A and 4.2A show herbivore abundance on 3 S. exigua and 3 Tamarix study plots from March, 1980 through July, 1985. Population increases in 1980 and 1984 occurred only on the two Tamarix sites that lay wholly in Zones A and B. Both of these years were characterized by relatively high flows of $1,100\text{m}^3/\text{sec}$ to $1,400\text{m}^3/\text{sec}$ and normal or above-normal summer precipitation. A slight increase in S2 herbivore abundance (and in Tamarix stands at Lees Ferry, and at the T1 and T2 sites) was also seen in 1985, a flood year with low summer precipitation. A lower magnitude population bloom occurred in 1985, suggesting that both precipitation and flooding contribute to Opsius outbreaks on Tamarix. The total invertebrate abundance was 467.9 insects/50 sweeps on S. exigua and 484.8 insects/50 sweeps on Tamarix, and not significantly different ($p = 0.914$, $df = 7$). Invertebrate herbivore abundance on both plant species declined with distance downstream in August, 1984 (Figures 4.3A and 4.4A), particularly on Tamarix.

Invertebrate Species Richness

Salix exigua supports three times as many species of phytophagous invertebrates as Tamarix in this system. Herbivore species richness varied significantly between these two plant species, with a mean of 12.13 species/50 sweeps on willow and 3.75 species/50 sweeps on Tamarix ($p < 0.001$, $df = 7$). Figure 4.1B and 4.2B show this pattern of higher species on three S. exigua study plots and three Tamarix study plots from March, 1980 to July, 1985. Total invertebrate species richness was also significantly higher on S. exigua (mean = 33.4) than on Tamarix (mean = 15.9) at $p = 0.004$ ($df = 7$). Invertebrate herbivore species richness on both plant species declined with distance downstream from Lees Ferry in August, 1984 (Figures 4.3B and 4.4B).

Community Structure and Similarity

Invertebrate herbivores were significantly more evenly distributed on S. exigua (mean $J' = 0.650$) than on Tamarix (mean $J' = 0.370$; $p = 0.043$, $df = 7$), again reflecting the strong dominance of Opsius on Tamarix (Appendix 4.1). In 1984 herbivore community similarity, as measured by SIMI comparisons, remained relatively constant for S. exigua through distance downstream from Lees Ferry, but community similarity declined with distance on Tamarix (Figure 4.5). Comparison of late-summer samples from 1982 with samples in subsequent years showed that community similarity declined on Salix plots from 1982 to 1984, and then rose again in 1985 (Figure 4.6). Causes for the decline in community similarity are related to extensive, prolonged inundation of Salix

stands in both 1983 and 1984, during which time phytophagous insects were literally washed off their host plants. High community similarity on S. exigua in 1985 indicated a rapid recovery of invertebrate herbivore populations. On Tamarix plots, SIMI remained high from 1982 through 1985 on T1 and T2, plots which lay wholly in Zones A and B. Tamarix plot T3 showed a decline in SIMI value in 1983 and 1984 and then a recovery in 1985. Because of their greater stature, Tamarix plants were often not completely inundated by high discharges in 1983, and the associated phytophagous insect retinue was afforded some refuge. Also, Stevens (1985) showed that, in part, the apparent stability of Tamarix herbivore communities was due to low species richness on this plant species.

Adult Forms of Aquatic Diptera

Aquatic larval Diptera emerge from the river and land on terrestrial riparian vegetation to rest and breed. Chironomid and, to a lesser extent, simuliid flies were regularly collected in sweep-net samples, and these species comprise a substantial proportion of the invertebrate resource base available to terrestrial vertebrates. To determine abundance and population fluctuations of aquatic Diptera through time, adult chironomid midge abundance was compared on two matched pairs of Tamarix and S. exigua study plots from 1980 through 1985 (Figure 4.7). Collections on Tamarix plot T2 (Mile 48.4R) were paired with contemporaneous collections on S. exigua plot S2 (Mile 50.2R) from July, 1980 to July 1985. Comparisons were also made with matched T1 (Mile 43.5L) and S1 (43.1L) samples from May, 1980 to May, 1983. Two or more chironomid species were represented in most samples.

Paired t-tests on pooled data show that chironomids were significantly more abundant on S. exigua (mean abundance/50 sweeps = 129.8, n=31) than on Tamarix (mean abundance/50 sweeps = 87.4, n= 31) at $p = 0.039$ (df = 30). Adult chironomids may land selectively on Salix over Tamarix because (1) Salix is a native plant species and/or is less biochemically offensive, and/or (2) Salix supports fewer arboreal vertebrate predators. From our observations, Sceloporus magister (Iguanidae) and many avian species forage arboreally far more often in Tamarix than in S. exigua.

Overall mean chironomid abundance on four study sites from 1980 to 1985 was 225.6/50 sweeps. Oneway analysis of variance of adult chironomid abundance/50 sweeps on these four plots varied significantly between years ($p = 0.004$, df = 5, 63). Duncan's multiple range test showed 1981 and 1985 had significantly higher chironomid abundance than did the other years. Discharge was slightly lower than normal in 1981, and 1985 was characterized by high flows, similar but not as prolonged as 1984. These results suggest a relationship between discharge regime and adult chironomid population on terrestrial riparian plants because years with high flows and large fluctuations in flow (1980 and 1983) produced the lowest adult chironomid populations, and extreme fluctuations may negatively affect Cladophora beds and therefore the chironomid populations that dwell in them. It is hoped that ongoing research in other quarters of this environmental assessment will cast more light on factors regulating chironomid populations, such as discharge fluctuation, turbidity, predation by fish, and climate.

Discussion

Flooding in 1983 in the Colorado River corridor in Grand Canyon removed or otherwise killed more than 50% of the vegetation below the 1,700m³/sec discharge stage. This vegetation supported a substantial community of largely host-specific phytophagous invertebrates. Removal of riparian vegetation proportionately reduced the biomass of invertebrate herbivores, a reduction in potential food resources with unknown consequences on higher trophic levels in this system.

Moderate levels of flooding (i.e. below 1,400m³/sec in 1980 and 1984) and normal or above-normal summer precipitation stimulated population increases among invertebrate herbivores on S. exigua and Tamarix in Grand Canyon. Increased plant growth following flooding is suggested as a likely cause for these population outbreaks, although experimental verification is needed. High levels of flooding depressed herbivorous invertebrate population levels by inundating entire plants (especially in the case of S. exigua) and washing invertebrates away. Invertebrate community similarity decreased markedly in 1983 on Tamarix and in 1984 on S. exigua, but thereafter recovered quickly. Changes in herbivore distribution patterns were minor on both plant species and community similarity between 1982 and 1985 remained generally high.

While flooding in 1983 reduced overall invertebrate biomass by removal of host plants, flooding did not greatly affect phytophagous invertebrate diversity on plant species whose populations remained relatively intact, such as Salix and Tamarix. Baccharis salicifolia and B. emoryi populations suffered large-scale reduction throughout much of the river corridor; however, these plant species naturally support only low densities and diversities of herbivore species, and it is unlikely that their contribution to overall invertebrate production is significant in this system.

Foliage feeding invertebrate populations appear to recover quickly from flooding disturbance; however, fossorial, geophilic and leaf-litter species (e.g. Arachnida, Collembola, Homoptera, Coleoptera, and ground-dwelling Hymenoptera) may be much slower to respond. We have little data on these guilds of invertebrates, but observations before and after flooding in 1983 indicated several trends. Reduction of S. exigua and other important cover species throughout the river corridor reduced habitat availability for ground-dwelling spiders, collembolans, and beetles. Until cover is restored on beaches, populations of many of these species will remain at low levels.

Harvester ants (Pogonomyrmex spp.) nest in diverse settings in this system, and were abundant on beaches prior to 1983. These scavengers forage on seeds and human refuse. Pogonomyrmex populations on beaches were severely reduced by flooding in 1983. Winged, reproductive adults emerge in July (Stevens 1976a) and colonize beaches at that time; however, repeated mid-summer flooding in 1984 and 1985 precluded recolonization by harvester or other ant species.

Apache cicadas (Diceroprocta apache) were extremely abundant in the river corridor prior to 1983, and this species is known to be a

preferred food resource for many birds (Glinski and Ohmart 1984). Root-feeding, fossorial cicada nymphs appear to require moderately well-drained soils with abundant root growth, and emerge in abundance in early summer (Stevens unpublished 1985). Prior to flooding in 1983, exuviae were abundant on all study plots and the droning buzz of adult male cicadas was heard throughout the river corridor. Following flooding in the summer of 1983 and 1984 adult cicadas were heard only rarely and exuviae were not found on any plants or study plots that had been inundated. At Mile 122.1R in 1982, cicada egg slashes were found on more than 90% of S. exigua stems. In 1984 and 1985, no ovipositional slashes were found on several hundred S. exigua stems examined in this area. From these observations we may surmise that nymphal Apache cicadas were drowned by floodwaters, and the population has been slow to recover.

Baccharis spp., Aplopappus acradenius, and other Compositae species bloom in the fall and, prior to flooding, supported large numbers of nectar-feeding Hymenoptera, such as Pompilidae, Sphecidae, and Chalcidoidea. Some of these wasp species, especially the Bembicine sphecids, prey on potentially noxious fly species (e.g. Calliphoridae and Sarcophagidae) that emerge in great abundance in spring and autumn. Reduction in flower availability (food resources) for these wasp species could not have improved their efficiency as predators, and may result in increased populations of pestiferous, non-biting flies in this system.

Elevated discharges in 1984 and 1985 left pools of standing water in many back-beach areas, and provided appropriate breeding habitat for mosquitoes (Culicidae). In 1984 and 1985 mosquitoes were noted at numerous sites where they had not been observed before, and were far more abundant than normal at sites such as Cardenas Creek and upper Unkar, where they occurred before. Similarly, pestiferous tabanid deer flies were far more common throughout the river corridor in 1984 and 1985 than they have been in the past ten years. Larval tabanids require moist substrates for growth, conditions which have been provided since 1983 by prolonged inundation. Populations of an intensely pestiferous "no-see-um" near Leptoconops (Diptera: Ceratopogonidae) were extremely high in the reach from Mile 220 to 226 in 1984 and 1985. Larval ceratopogonids require moist substrates provided by continuous, prolonged discharges. All of these observations suggest that populations of pestiferous Diptera in this system respond positively to flooding, and represent an unwelcome source of human discomfort.

Elevated discharges stimulated population explosions of at least two other insect species in this system. Prior to 1983 a large, aquatic hydrophilid beetle, Hydrophilis (triangularis?) was rare in this system and restricted to tributaries, particularly in the lower half of Grand Canyon. In 1984 and 1985 standing pools of water left by receding high discharges provided suitable habitat for this species along the river, and both larvae and adults were commonly encountered throughout the river corridor. Prior to 1983 trydactylid crickets occurred only in tributary riparian settings in the Grand Canyon. Following subsidence of elevated discharges in 1985, a population outbreak of tridactylids was observed on riverside beaches in the lower Canyon. This outbreak

was of sufficient magnitude to cause discomfort to commercial recreationists. This was the first outbreak of this species in twelve years of observation.

Aquatic and Terrestrial Trophic Interactions

We compiled a food-web diagram for the Colorado River riparian ecosystem using information gathered over the past decade of research and observation in Grand Canyon (Figure 4.8). This diagram is, as yet, non-quantitative, but indicates actual and probable trophic relationships between the aquatic and terrestrial aspects of this system. Several points from this diagram merit discussion.

First, the aquatic and terrestrial components of this system are intimately related. Flooding of the river promotes erosion (Stevens, unpublished 1982), substrate leaching, and increased terrestrial plant mortality near the river, and may stimulate vegetation growth on pre-dam terraces (Ruffner and Anderson, this assessment).

Secondly, higher trophic level terrestrial omnivores and insectivores depend on adult aquatic Diptera as food resources in this system. Chironomid midges and simuliid gnats probably comprise much of the diets of aerially-feeding swifts, swallows, and perhaps of hummingbirds in the river corridor. Swallows dissected in 1975 by one of us showed extensive infestations of muscle cysts, and such parasites may be vectored by chironomid midges (this requires further study). Insectivorous Bufo spp. toads, and Cnemidophorus, Uta, Urosaurus, and Sceloporus lizards feed heavily on adult aquatic Diptera, and Pogonomyrmex ants have been observed harvesting simuliids, especially during periods when seeds are scarce. Additionally, Cnemidophorus and probably other lizards, as well as several avian species, forage along the water's edge and harvest stranded Gammarus.

While the pattern of aquatic resource use by terrestrial species is clear, the role of terrestrial invertebrates in this system has not been established. The extent to which semi-aquatic and terrestrial toads, lizards, birds, and rodents depend on terrestrial invertebrates (especially ground-dwelling and phytophagous species) is not known. As indicated above, outbreaks of phytophagous Heteroptera on dominant plant species may represent an equally valuable food resource for vertebrate insectivores in this system. Future research should include specific studies of trophic interactions and quantification of energy flow in this system to determine the importance of the aquatic ecosystem components to the terrestrial components, and vice versa.

Disturbance from flooding directly or indirectly affects most, if not all, of the terrestrial species and processes in this riparian system. It is imperative that discharge management criteria include consideration of impacts on the terrestrial components of this system. We have tried to demonstrate some of the problems engendered by erratic high releases in this system, and encourage managers to carefully consider operating criteria that protect and improve the value of the post-dam riparian vegetation zone in Grand Canyon.

Conclusions

The following conclusions are drawn from this portion of the study:

1. Because of the extensive flood-induced loss of riparian vegetation and substrate in this system, a substantial proportion of the total biomass of phytophagous, terrestrial, and fossorial riparian invertebrate life was lost in 1983.
2. Outbreaks of invertebrate herbivores on Tamarix and, to a lesser extent, Salix exigua, are correlated with moderate levels of flooding and adequate summer precipitation in this system. Normal (pre-1983) and high (e.g. 1983) discharges and low summer precipitation (e.g. 1985) resulted in low densities of invertebrate herbivores. This correlation should be tested experimentally before it is used as a management criterion.
3. Flooding temporarily decreased invertebrate herbivore species richness on Salix exigua, but not on Tamarix in this system. Phytophagous invertebrate populations generally recovered from flooding quickly. As compared to 1982, invertebrate herbivore community similarity declined in 1983 and 1984 on Salix exigua but remained relatively constant on Tamarix. In 1985 levels of community similarity were comparable to 1982 levels.
4. Phytophagous invertebrate community similarity declined with distance downstream from Glen Canyon Dam for Tamarix but not for Salix exigua.
5. Adult chironomid midges were observed to comprise a significant proportion of the food resources available to predaceous insects, amphibians, reptiles, and birds in this system. Chironomids prefer to alight on Salix rather than Tamarix, and adult chironomid populations were lowest during years of high flows and large fluctuations (1980 and 1983).
6. Changes in the population dynamics of several insect taxa were observed or inferred following post-1982 alterations in the discharge regime in this system. Orthopteran (e.g. Tridactylidae), Coleopteran (e.g. Hydrophilis), and pestiferous Diptera (e.g. Ceratopogonidae and Tabanidae) populations increased, while Hymenoptera (especially ants and sphecids wasps) populations declined.
7. Trophic interactions between the riverine and terrestrial components of this ecosystem are complex and closely inter-related. Management of terrestrial resources in the Colorado River corridor in Grand Canyon will require a detailed appreciation of the major inter-relationships between these components.

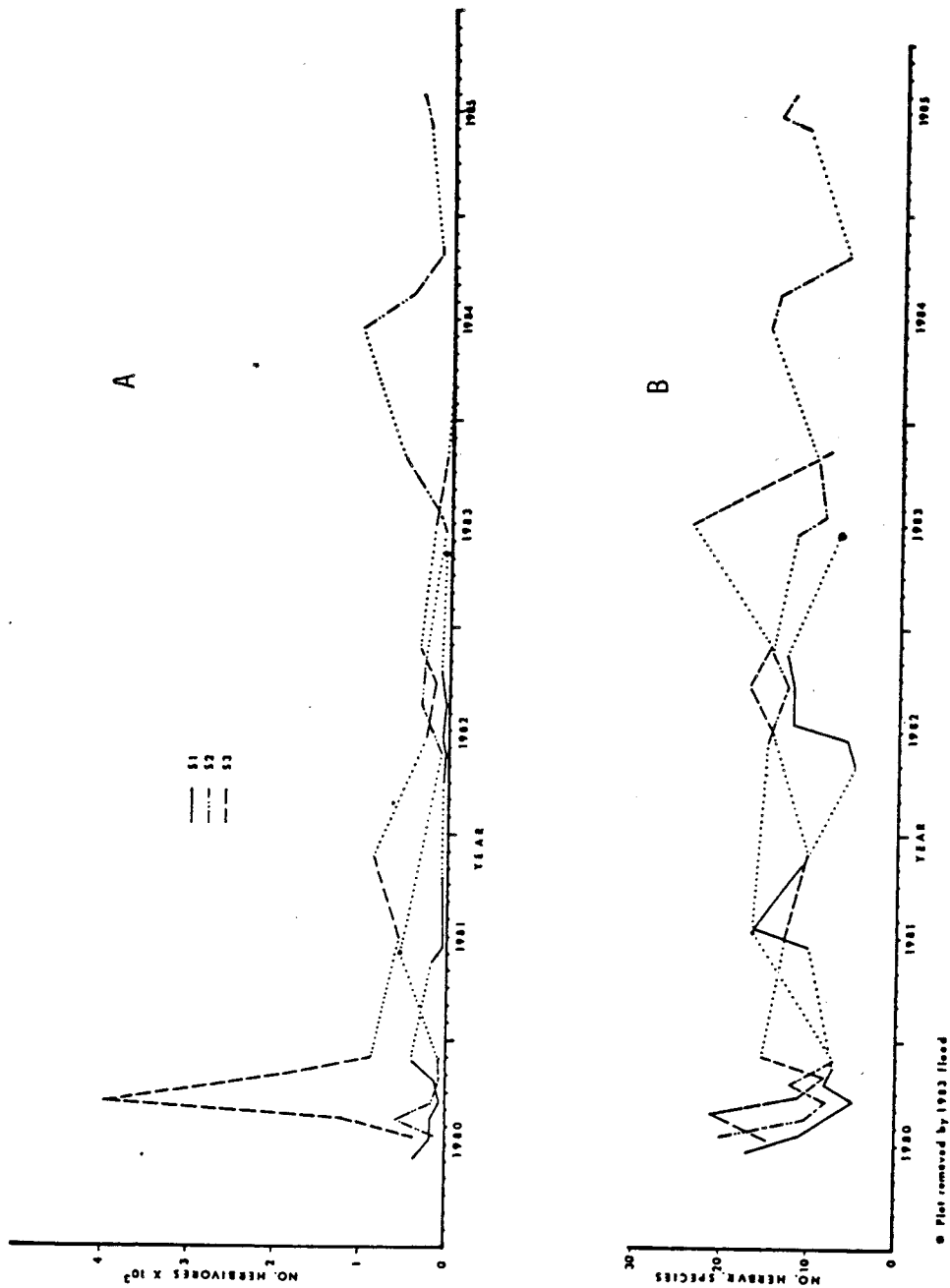


FIGURE 4.1A: PHYTOPHAGOUS INSECT ABUNDANCE/50 SWEEPS ON THREE SALIX EXIGUA STUDY PLOTS, 1980-1985.

B: PHYTOPHAGOUS INSECT SPECIES RICHNESS/50 SWEEPS ON THREE SALIX EXIGUA STUDY PLOTS, 1980-1985.

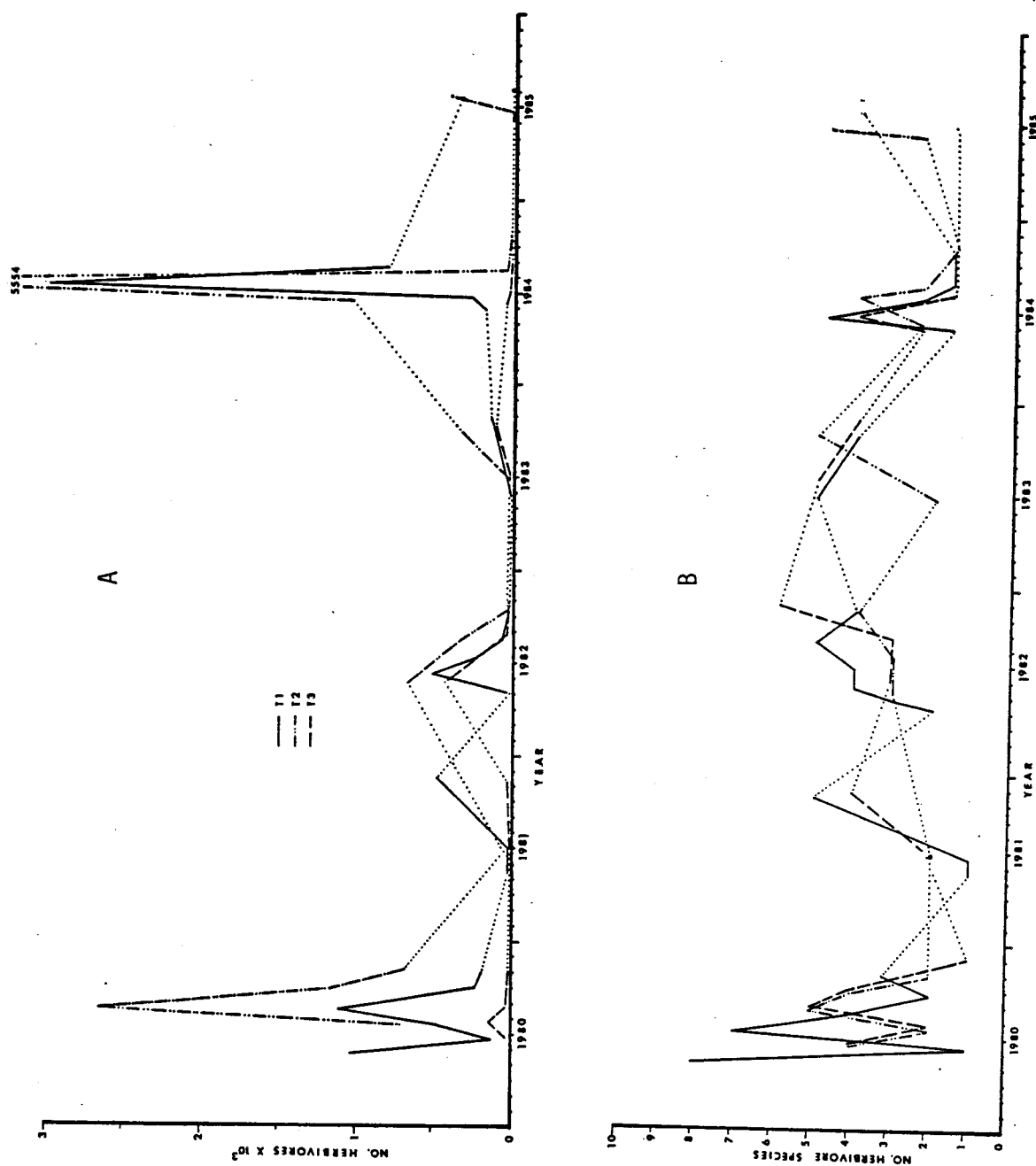


FIGURE 4.2A: PHYTOPHAGOUS INSECT ABUNDANCE/50 SWEEPS ON THREE TAMARIX CHINENSIS STUDY PLOTS, 1980-1985.

B: PHYTOPHAGOUS INSECT SPECIES RICHNESS/50 SWEEPS ON THREE TAMARIX CHINENSIS STUDY PLOTS, 1980-1985.

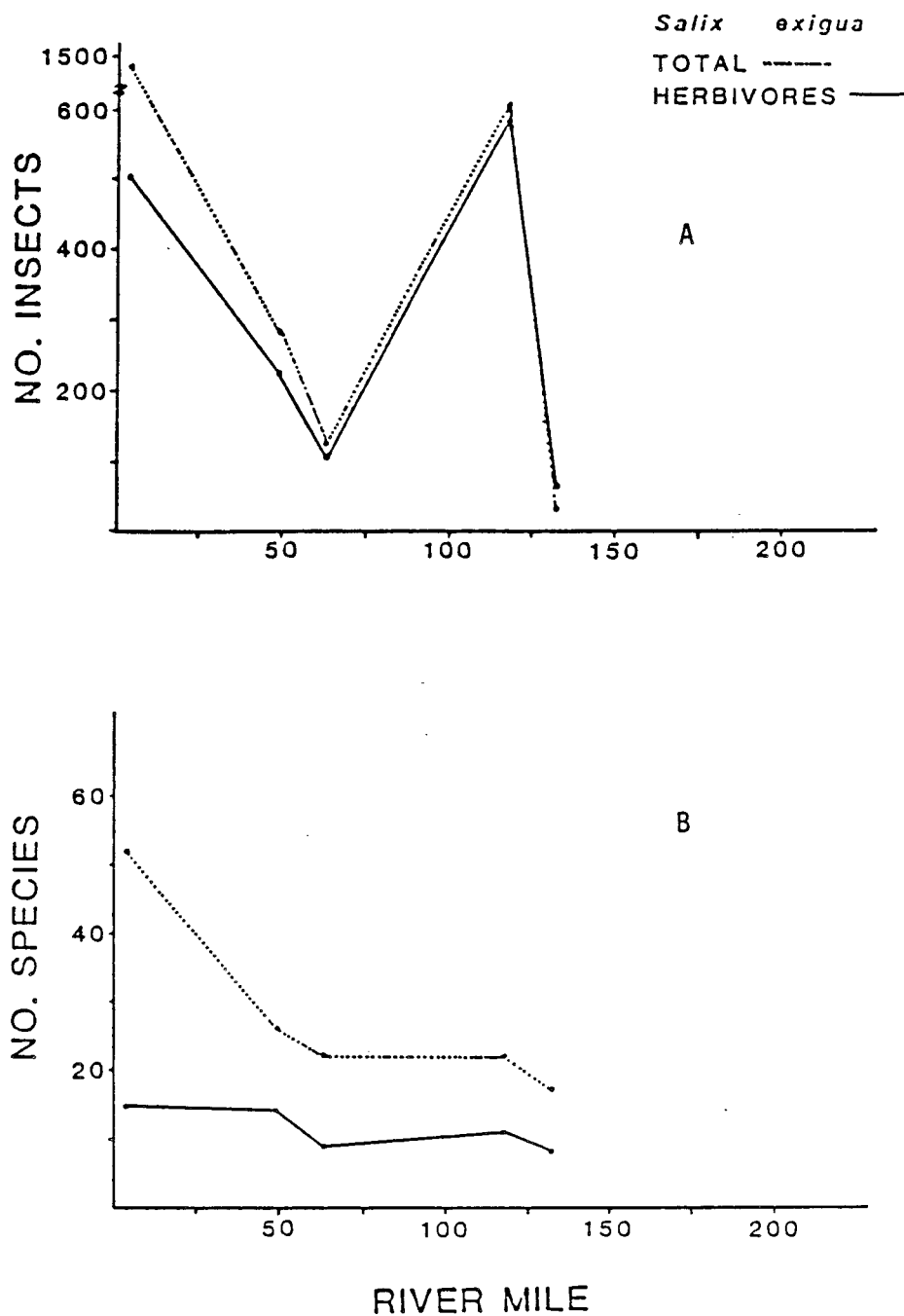


FIGURE 4.3A: PHYTOPHAGOUS INSECT ABUNDANCE/50 SWEEPS ON SALIX EXIGUA BY DISTANCE DOWNSTREAM FROM LEES FERRY IN MID TO LATE AUGUST, 1984.

B: PHYTOPHAGOUS INSECT SPECIES RICHNESS/50 SWEEPS ON SALIX EXIGUA BY DISTANCE DOWNSTREAM FROM LEES FERRY IN MID-TO LATE AUGUST, 1984.

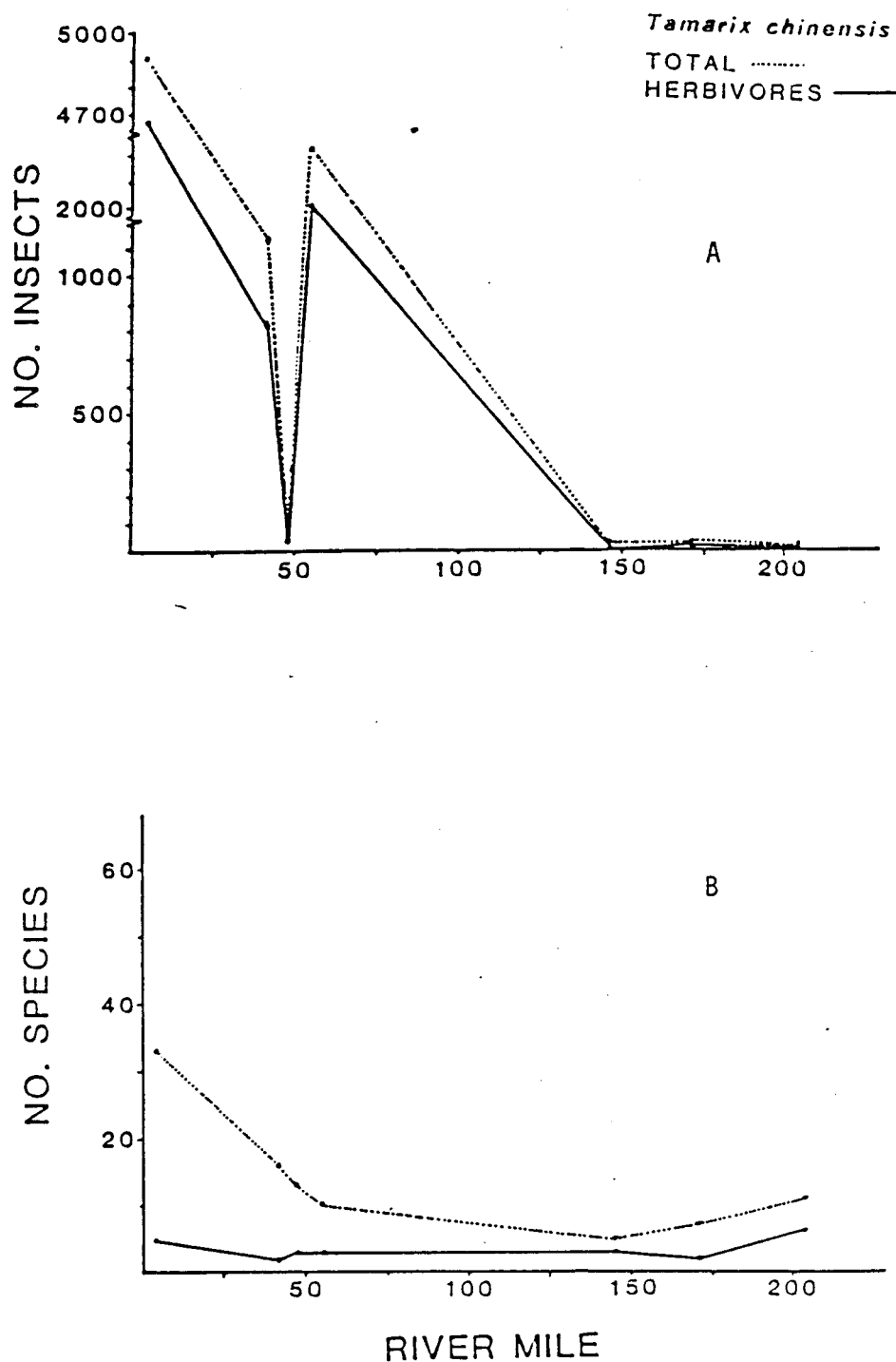


FIGURE 4.4A: PHYTOPHAGOUS INSECT ABUNDANCE/50 SWEEPS ON TAMARIX CHINENSIS BY DISTANCE FROM LEES FERRY IN MID TO LATE AUGUST, 1984.

B: PHYTOPHAGOUS INSECT SPECIES RICHNESS/50 SWEEPS ON TAMARIX CHINENSIS BY DISTANCE DOWNSTREAM FROM LEES FERRY IN MID TO LATE AUGUST, 1984.

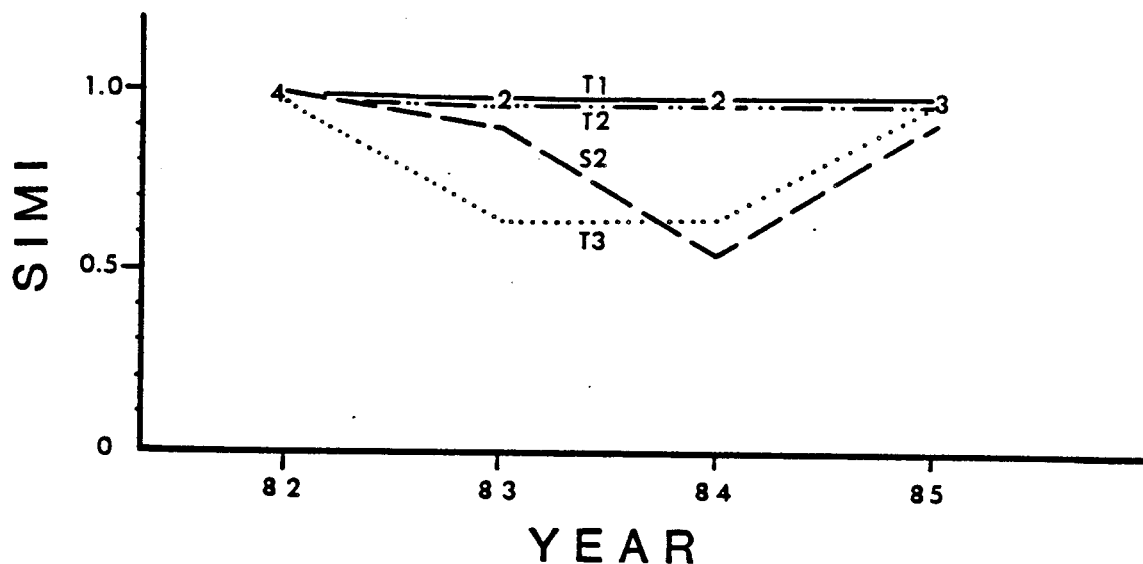
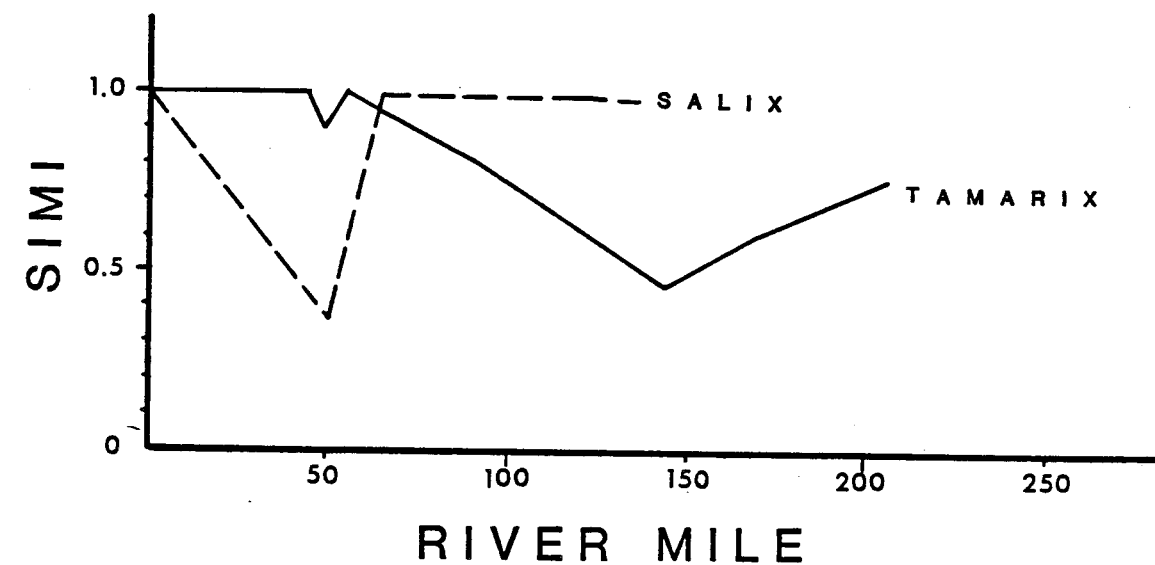


FIGURE 4.5: CHANGE IN COMMUNITY SIMILARITY (STANDER, 1970) OVER DISTANCE FROM LEES FERRY FOR SALIX EXIGUA AND TAMARIX CHINENSIS PHYTOPHAGOUS INSECT COMMUNITIES, AUGUST 1984.

FIGURE 4.6: CHANGE IN COMMUNITY SIMILARITY THROUGH TIME, USING STANDER'S (1970) INDEX ON LATE SUMMER HERBIVOROUS INSECT DATA ON ONE SALIX EXIGUA AND THREE TAMARIX CHINENSIS STUDY SITES.

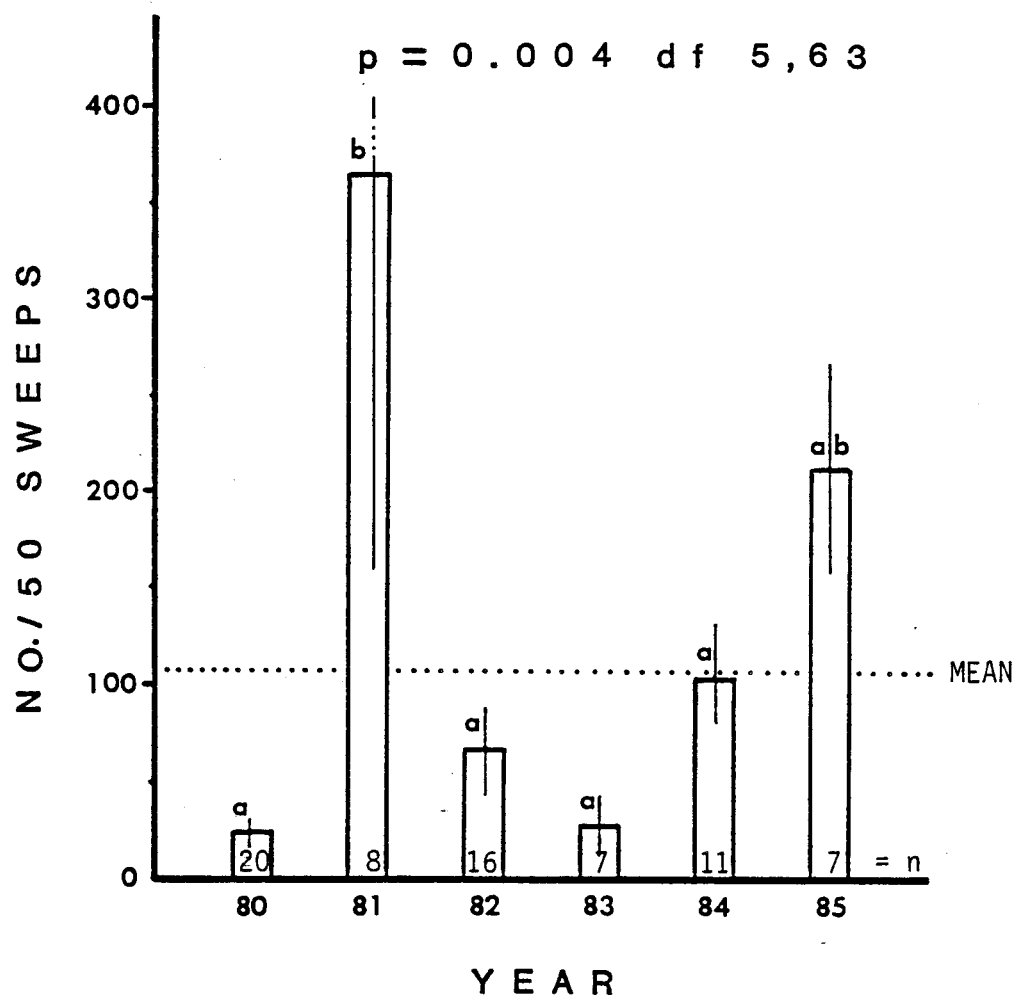


FIGURE 4.7: MEAN CHIRONOMID ABUNDANCE ON FOUR STUDY SITES FROM 1980 THROUGH 1985.

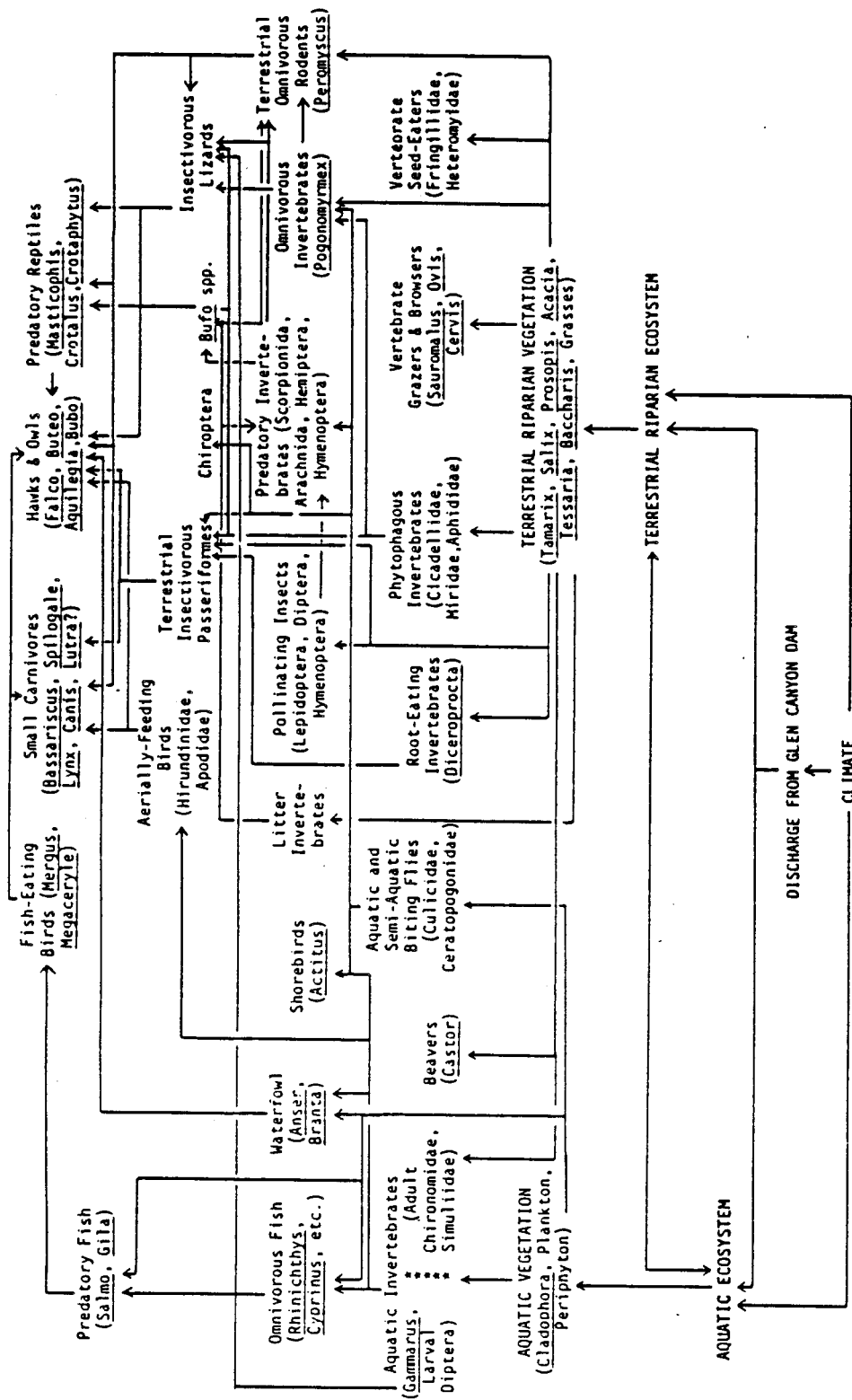


FIGURE 4.8: OBSERVED AND PROBABLE INTERACTIONS BETWEEN AQUATIC AND TERRESTRIAL COMPONENTS IN THE COLORADO RIVER RIPARIAN ZONE IN GRAND CANYON.

CHAPTER V: OPERATING CRITERIA

In this chapter we review and discuss the Bureau of Reclamation's five flow regime alternatives proposed for Glen Canyon Dam (Wegner 1985).

Alternative 1: Monthly base-loaded power plant releases.

A base-loaded flow scenario is preferred for the riparian ecosystem in Grand Canyon. Such a flow regime would (1) minimize leaching and loss of base cations, nutrients, and fine particle riparian substrates; (2) minimize scouring removal and drowning of riparian vegetation; (3) promote survival of established seedlings; and (4) encourage stability of native invertebrate populations.

Alternative 2: Status quo with maximized power releases.

This alternative would prevent successful reestablishment and survival of native riparian plant species in the floodzone where that vegetation could be most prolific. Continued leaching and loss of nutrients and fine particles would be promoted by such a flow regime, and would bring a continued decline in habitat quality for riparian plant life. Extreme daily fluctuations may promote rapid leaching from beach and bank substrates as much as several meters above the water line (Birkeland, 1984).

Alternative 3: Maximized power plant releases between 8,000cfs and 25,000cfs.

This "limited disturbance" alternative is somewhat more conducive to vegetation growth than is Alternative 2 (above). If erosion could be alleviated by slowing the rate of change in discharge, this flow regime could have a relatively minor negative impact on the terrestrial ecosystem.

Alternative 4: Seasonally base-loaded flows with maximized power releases in other seasons.

This alternative may be suitable for recreational interests but it is not recommended for the riparian ecosystem because of the impacts of leaching and loss of fine particle sediments, the loss of vegetation, and the destabilizing influence it would exert on the riparian ecosystem.

Alternative 5: Maximized fishery releases.

This alternative is not recommended for the reasons discussed under Alternative 2 (above).

The Timing of Spillovers

In the event of future spills in this system, the timing of spills could conceivably be used to facilitate establishment of native plant species, which produce seeds in the middle and late summer, over exotic Tamarix, which produces most of its seed load in May and June. Spring flooding may reduce invertebrate populations for a month or more after subsidence, and riparian invertebrates are used extensively as food by terrestrial vertebrates, particularly amphibians, reptiles, and birds.

Spring flooding may negatively impact resource availability for these vertebrates, and of special importance is resource availability for nesting birds and reproductive amphibians and reptiles. While flooding exerts negative effects on resources (invertebrate populations) regardless of the season, flooding should be avoided during the peak reproductive season for vertebrates.

Low water years have been shown by Stevens (unpublished 1985) to exert negative impacts on Salix exigua growth. The preferred alternative for low flow years is higher releases during the hottest, driest months (late May through mid-July) to protect established plants from dessication.

From a practical standpoint we recognize the difficulty of multiple use discharge management in this system; however, spillover releases 1) wreak havoc on the riparian ecosystem, 2) are wasteful, and 3) are potentially damaging to Glen Canyon Dam. The biotic and recreational value of the Colorado River riparian corridor in Grand Canyon justifies its inclusion as a resource worthy of preservation. Protection and improvement of this riparian system can only be achieved through a carefully considered policy of discharge management. We hope that this report contributes to an improved understanding and dialogue concerning proper management of this system.

CHAPTER VI: GENERAL CONCLUSIONS

Dam Effects on the Colorado River Corridor

Riparian lands have repeatedly been shown to be the most valuable and yet the most abused habitats in the Southwest (Johnson and Jones 1977; Johnson and Carothers 1982; Johnson et al. 1985). The construction of Glen Canyon Dam created a riparian habitat of considerable worth to wildlife and recreation (Carothers and Aitchison 1976; Turner and Karpiscak 1980; Stevens unpublished 1985) and the responsibility for the well-being of this riparian ecosystem rests squarely on the shoulders of the Bureau of Reclamation and the National Park Service. We wish to emphasize the need for intentional management in this system, not accidental erratic discharges that are detrimental to the environmental quality and value of this riparian ecosystem.

In Grand Canyon, low magnitude flooding (relative to the "normal", 1963-1979 flow) in 1980, resulted in increased beach erosion but initiated a short-lived germination event (Stevens unpublished 1982 and 1985). Catastrophic flooding in 1983 had at least three direct effects on the terrestrial riparian ecosystem. First, flooding was a leaching event, resulting in marked decreases in substrate base cation concentrations, particularly monovalent cations, reduced organic matter, and reduced proportions of fine particle clays and silts in inundated substrates. Minor changes in substrate pH accompanied this event. These substrate changes promote an increased rate of erosion of beach sands and reduce the nutritive value and water-holding capacity of beach sands, thereby reducing the quality of the habitat for seedling and adult riparian plants.

Secondly, flooding removed or drowned more than 50% of the riparian plants below the estimated 1,700m³/sec stage, the zone in which post-dam vegetation was formerly most profuse. Total mortality rates were highest near the river and on sand and cobble substrates, and were strongly differential, with Tamarix, Salix spp., Acacia, Phragmites, Aster spinosus and Tesssaria sericea faring better than Prosopis, Typha, Baccharis spp. and Brickellia. While no plant species were lost from the river corridor by this flooding event, the evenness of distribution of species declined slightly but significantly because of disproportionate declines in the abundance of certain species. Post-flood germination was observed on many sites, and continued in 1984 and 1985. Return of discharge levels to pre-1983 "normal" levels (85-820m³/sec) may strand many of the surviving recruits above the capillary fringe, and increase seedling mortality.

Thirdly, flooding in this system affected insect community dynamics in many ways. Populations of phytophagous invertebrates on Tamarix and Salix were directly reduced by flooding. Unlike S. exigua, Tamarix occupies non-inundated Zone D in this system, and populations of phytophagous insects on Tamarix--notably that of Opsius stactogalus--quickly reinvaded and reached outbreak proportions in 1984. Flooding reduced populations of fossorial and ground-dwelling invertebrates, including harvester ants, Apache cicadas, and other important taxa.

Recognizing the value of this riparian corridor for recreation and wildlife, and the need for appropriate, intentional management, how can the operation of Glen Canyon Dam prolong or facilitate the well-being of this system? The flow regime of Glen Canyon Dam directly controls the development of terrestrial riparian vegetation and riparian community processes in this system. From the standpoint of biotic development in Zone A and B, disturbance (erratic high flows and erosion) should be kept at a minimum to maximize biological activity and to facilitate the process of vegetational succession. Stevens (unpublished 1985) found that understory species diversity and biomass increased rapidly from July, 1980 to May, 1983 (a period of relatively "normal" post-dam flows), particularly beneath stands of Salix exigua. This recruitment event was promoted by a relatively brief, $1,400\text{m}^3/\text{sec}$ flood in 1980, and was terminated by extreme discharges in 1983. Rare, low magnitude/short duration flooding may be of value in promoting germination in riparian habitats; however, riparian shrub and tree seedlings require at least several years to mature to the point where they can withstand the direct consequences of such flooding (Kozlowski 1984; Stevens and Waring, 1985). Rare flooding might encourage decomposition of organic matter in the substrate as well. Therefore, a flow scenario with an established maximum discharge level--one that minimizes bank-cutting erosion--with rare, low magnitude/short duration floods is considered best. By "rare" we mean occurring on the order of once every 10 to 20 years. The results of ongoing successional studies in this system should indicate the schedule for such flooding events.

GLOSSARY

atomic absorption spectrophotometry a technique for the measurement of ion concentrations through ignition and comparison of absorption or emission of specific light wavelengths against a known standard.

alluvium geologic materials moved by water.

analysis of variance a statistical technique that compares the means of two or more sets of data.

anoxic without free oxygen.

base cations the positively charged mineral ions sodium (Na^+), potassium (K^+), calcium (Ca^{++}), and magnesium (Mg^{++}).

biomass the wet or dry total mass of biological material (usually of a given taxon) per unit area.

buffer mitigation of change, specifically in pH.

capillary rise the elevation of water in a porous substrate through capillary action.

carbonate consisting largely of the mineral, calcium carbonate: CaCO_3

Chi² test a statistical test that compares observed with expected values.

clone vegetative (asexual) generation of somatic tissue.

colluvial geologic materials moved by gravity.

community a group of ecologically interacting populations.

disturbance a change in biotic and/or abiotic environmental conditions.

divalent having a double, positive ionic charge.

Duncan's multiple range test a statistical test that indicates specific relationships between the means of three or more data sets.

edaphic relating to the soil, especially from the standpoint of vegetational requirements

entisol a soil order composed of young, unweathered soils with no O or A horizons.

eolian relating to the wind.

evenness an ecological measure of the relative abundance of species within a community (e.g. J').

exotic introduced, not native.

fluvial having to do with rivers.

fossorial burrowing or otherwise dwelling in the soil.

gleyed a pedological condition in which chemical changes occur in a soil depleted of free oxygen.

halophilic highly salt tolerant.

haplustoll a soil type occurring in a moderately arid climatic regime, having moderate levels organic matter, and some profile development

hydrometer an instrument that measures the specific gravity of a fluid.

inceptisol a soil order consisting of relatively young substrates with an O and/or a partially developed A horizon.

macrophyte an emergent aquatic plant.

mesic moist.

meteoric derived from atmospheric sources.

mollisol a soil order consisting of old, well developed horizons, especially with well defined O, A, and B horizons.

monovalent having a single positive ionic charge.

niche an n-dimensional ecological hypervolume, the biotic and abiotic environment occupied by a species.

organic matter that portion of the substrate consisting of decomposed and partially decomposed biological materials.

outbreak large, rapid expansion of a population.

pedology the study of soils and soil evolution.

pH the negative logarithm of hydrogen ion concentration; low pH means high acidity and high pH means high alkalinity.

phosphorus binding complexing of phosphorus to other minerals.

principle components analysis statistical determination of the most important factors affecting a variable.

regression a statistical linear correlation of one variable with another

riparian streamside.

riffle a small rapid, usually bedded by cobbles.

species diversity a community ecology statistic that combines species richness and species abundance.

species richness the number of species in a community.

statistical significance the probability that an observation is not due to chance; the probability that the variability between two or more sets of data is not due to chance. In this study, the level of this probability was set at 95%.

succession (predictable) change in the structure and species composition of an ecological community.

t-test (paired) statistical comparison of the means of paired sets of data; used especially with small data sets.

texture (soil) the percent of gravel or rock, sand, silt, and clay in a soil sample.

torrifuvent a young, unweathered soil deposited in an arid environment by fluvial hydrologic processes.

transformation (of data) a technique in linear regression to stabilize the variance of a data set.

trophic structure the food web of an ecological community.

turbidity reduction of light transmission, usually by suspended or dissolved sediments in (flowing) water.

vortex a mechanical technique involving rapid spinning for mixing.

xeric desert adapted.

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APPENDIX 2.1:
GRAND CANYON RIPARIAN ZONE EDAPHIC DATA, 1984.

MILE/SIDE (SITE#):	0.1R (1)	COLLECTION DATE	21-VI-84	REACH TYPE:	Straight	STAGE:	ca.3400m ³ /s
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COVER TYPE(1981): Dense Tamarix COVER TYPE (1984): Dense Tamarix

PROFILE: 0-31cm fine sand, slightly bedded
31-31.5cm dark (organic?) band
31.5-45cm redder, slightly more coarse sand
45-45.5cm dark band
45.5-150cm redder sandy silt

Roots mostly in upper 100cm
This site was not inundated in 1983.

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE CHEMISTRY					SUBSTRATE TEXTURE				% ORGANIC + CARBONATES	
	pH	Na ⁺ (μg/g)	K ⁺ (μg/g)	Ca ⁺² (μg/g)	Mg ⁺² (μg/g)	TOTAL CATIONS (μg/g)	% GRAVEL	% SAND	% SILT+CLAY		% CLAY
5	8.4	393.6	213.7	1695	229.6	2531.9	0.0	77.7	22.2	0.6	9.999
35	8.1	497.5	56.0	1499	218.7	2271.2	0.0	67.7	32.3	1.2	0.485
(81) 35	7.7	956.8	52.3	1517	273.4	2799.5	0.0	36.2	63.9	8.0	1.804
50	8.1	956.8	53.0	1977	377.2	3364.0	0.0	38.7	61.3	5.2	9.999
75	8.0	544.9	51.3	1490	240.6	2326.8	0.0	80.5	19.5	1.8	9.999
100	7.8	362.7	41.2	1572	273.4	2249.3	0.0	72.9	27.1	3.6	9.999
150	8.0	965.9	49.3	1791	470.2	3276.4	0.0	26.0	74.1	4.8	9.999
AVG	8.1	620.2	77.4	1671	301.6	2670.2	0.0	60.6	39.4	2.9	9.999

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COVER TYPE(1981): Dense Tamarix COVER TYPE (1984): Dense Tamarix

18-21cm red sandy silt (flashflood?)

21-25cm silty sand

25-27cm red sandy silt

27-45cm silty sand

45-50cm darker, organic horizon

50-100cm silty sand

100-110cm white silt hardpan

110-150cm silty sand

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE CHEMISTRY					TOTAL CATIONS (μg/g)	SUBSTRATE TEXTURE				% ORGANIC + CARBONATES
	pH	Na ⁺ (μg/g)	K ⁺ (μg/g)	Ca ⁺² (μg/g)	Mg ⁺² (μg/g)		% GRAVEL	% SAND	% SILT+CLAY	% CLAY	
5	8.2	235.1	368.6	1517	331.7	2452.4	0.0	40.6	59.3	1.4	9.999
35	8.0	464.7	50.0	1540	331.7	2386.4	0.0	11.1	88.7	5.4	2.156
(.81) 35	7.5	457.4	254.5	1690	608.7	3010.6	0.0	36.9	63.2	11.0	1.736
50	8.1	48.3	89.8	1599	238.7	1975.8	0.0	37.4	62.6	0.2	9.999
75	8.2	45.9	94.2	1358	311.6	1809.7	0.0	13.9	86.1	4.0	9.999
100	8.3	38.8	74.9	1549	262.4	1925.1	0.0	53.0	47.0	1.6	9.999
150	7.8	63.5	78.0	1581	297.1	2019.6	0.0	12.1	87.9	4.2	9.999
AVG	8.1	149.4	125.9	1524	295.5	2094.8	0.0	28.0	71.9	2.8	9.999

1984 GRAND CANYON RIPARIAN ZONE EDAPHIC DATA

MILE/SIDE (SITE#): 1.2R (3) COLLECTION DATE 2-IX-84 REACH TYPE: Eddy STAGE: ca. 700m³/s
COVER TYPE(1981): Dense Salix ex. COVER TYPE (1984): Sparse Salix exigua

PROFILE: 0-7cm moderately coarse sand (eolian?)
7-24cm sandy silt, progressively darker with depth
24-33cm eolian? sand
33-57cm sandy silt
57-59cm organic, dark band
59-65cm sandy silt
65-67cm organic, dark band
67-125cm sandy silt
125cm water

Roots to 35cm, with some larger, pre-1983 roots. This site was inundated in 1983.

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE CHEMISTRY				SUBSTRATE TEXTURE			
	pH	Na ⁺ (μg/g)	K ⁺ (μg/g)	Ca ²⁺ (μg/g)	Mg ²⁺ (μg/g)	TOTAL CATIONS (μg/g)	% GRAVEL	% SAND
5	8.2	29.7	19.9	1522	235.1	1806.7	0.0	92.2
35	8.3	39.8	31.0	1453	173.1	1696.9	0.0	72.8
('81) 35	8.3	6.4	10.8	1034	260.6	1311.8	0.0	99.6
50	8.2	9.8	8.1	633	156.7	807.6	0.0	100.0
75	8.0	16.9	14.5	1116	246.0	1393.4	0.0	99.9
100	8.1	26.0	22.6	1144	189.5	1382.1	0.0	99.5
125	8.3	16.9	13.2	1084	184.1	1298.2	0.0	100.0
AVG	8.2	23.2	18.2	1159	197.4	1397.8	0.0	94.1
							% SILT+CLAY	% CLAY
							7.7	1.2
							27.1	2.2
							0.4	3.3
							0.0	2.8
							0.2	0.0
							0.5	4.6
							0.1	0.8
							5.9	1.9
								% ORGANIC + CARBONATES
								9.999
								0.728
								0.809
								9.999
								9.999
								9.999
								9.999

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COVER TYPE(1981): Unvegetated COVER TYPE (1984): Unvegetated

**Roots through upper 100cm.
This site was not inundated in 1983.**

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE CHEMISTRY					TOTAL CATIONS (µg/g)	SUBSTRATE TEXTURE				% ORGANIC + CARBONATES
	pH	Na ⁺ (µg/g)	K ⁺ (µg/g)	Ca ⁺² (µg/g)	Mg ⁺² (µg/g)		% GRAVEL	% SAND	% SILT+CLAY	% CLAY	
5	8.3	8.4	127.9	1654	147.6	1937.9	37.5	59.0	5.5	1.7	9.999
35	7.9	148.5	22.6	1380	295.2	1846.3	0.0	82.4	17.6	1.4	0.699
50	8.2	461.1	24.8	1543	329.8	2358.7	0.0	56.8	43.3	2.2	9.999
75	8.3	26.3	354.4	1677	220.5	2278.2	0.0	34.4	65.5	6.0	9.999
100	8.0	142.8	91.1	1636	244.2	2114.1	0.0	7.3	92.6	7.6	9.999
150	7.9	46.9	47.6	1376	216.9	1687.4	0.0	73.9	26.2	3.0	9.999
AVG	8.1	139.0	111.4	1544	242.4	2036.8	6.3	52.3	41.8	3.7	9.999

1984 GRAND CANYON RIPARIAN ZONE EDAPHIC DATA

MILE/SIDE (SITE#): 3.1R (5) COLLECTION DATE 23-X-84 REACH TYPE: Eddy STAGE: ca. 1400m³/s

STAGE: ca. 1400m³/s

REACH TYPE: Eddy

COLLECTION DATE 23-X-84

3.1R (5)

COVER TYPE (1984): Open Beach

COVER TYPE(1981): Open Beach

PROFILE: 0-19cm fine sand, slightly bedded
19-24cm slightly siltier sand
24-75cm fine sand, slightly bedded
75cm rock

No roots here, as it is a fresh deposit of sand. This site was inundated in 1983.

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE		CHEMISTRY		SUBSTRATE TEXTURE					% ORGANIC + CARBONATES
	Na ⁺ (μg/g)	K ⁺ (μg/g)	Ca ⁺² (μg/g)	Mg ⁺² (μg/g)	TOTAL CATIONS (μg/g)	% GRAVEL	% SAND	% SILT+CLAY	% CLAY	
5	13.2	38.1	1303	156.7	1511.0	0.0	98.5	1.5	1.0	9.999
35	11.1	14.2	1435	160.4	1620.7	0.0	96.2	3.9	1.0	0.281
50	12.3	14.2	1278	152.2	1456.7	0.0	97.7	2.3	1.4	9.999
75	62.5	55.0	1367	171.3	1655.8	0.0	97.6	2.3	0.4	9.999
AVG	24.8	30.4	1346	160.2	1561.4	0.0	97.5	2.5	1.0	9.999

MILE/SIDE (SITE#): 34.2L (6) COLLECTION DATE 14-VIII-84 REACH TYPE: Small Eddy STAGE: ca. 1000m³/s

COVER TYPE(1981): Tamarix & Salix COVER TYPE (1984): Tamarix

PROFILE: 0-20cm silty sand with several 3-6cm bands of brown silt and 2 red bands
20-95cm moderate (eolian?) sand
95-100cm increasing organic matter, including branches. A reducing environment.
100cm breccia

This site appears to have slumped down onto itself following erosion in 1983. This site was inundated in 1983.

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	PH	SUBSTRATE CHEMISTRY				TOTAL CATIONS ($\mu\text{g/g}$)	SUBSTRATE TEXTURE				% ORGANIC + CARBONATES
		Na^+ ($\mu\text{g/g}$)	K^+ ($\mu\text{g/g}$)	Ca^{+2} ($\mu\text{g/g}$)	Mg^{+2} ($\mu\text{g/g}$)		% GRAVEL	% SAND	% SILT+CLAY	% CLAY	
5	8.1	40.2	40.5	1385	236.9	1702.6	0.0	63.6	36.4	4.2	9.999
35	8.1	32.7	22.6	1554	176.8	1786.1	0.0	86.4	13.6	0.4	0.632
35	7.5	44.9	42.2	1563	287.9	1938.0	0.0	49.0	50.9	9.3	2.010
50	8.0	30.4	28.4	1458	198.6	1715.4	0.0	79.8	20.2	2.0	9.999
75	8.2	35.4	37.5	1462	202.3	1737.2	0.0	79.6	20.3	0.0	9.999
100	7.8	60.4	69.2	1877	244.2	2250.8	10.0	53.8	36.3	3.2	9.999
AVG	8.0	39.8	39.6	1547	211.8	1838.2	2.0	72.6	25.4	2.0	9.999

1984 GRAND CANYON RIPARIAN ZONE EDAPHIC DATA

MILE/SIDE (SITE#): 41.2R (7) COLLECTION DATE 20-X-84 REACH TYPE: Large Eddy STAGE: ca. 500m³/s

COVER TYPE(1981): Salix - Typha COVER TYPE (1984): Open Beach

PROFILE: 0-145cm slightly cross-bedded medium fine sand
145cm water

This site has been deflated ca. 100cm from its pre-1983 level, and all vegetation has been scoured away. No roots encountered. This site was inundated in 1983.

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE CHEMISTRY				SUBSTRATE TEXTURE				% ORGANIC + CARBONATES		
	pH	Na ⁺ (µg/g)	K ⁺ (µg/g)	Ca ⁺² (µg/g)	Mg ⁺² (µg/g)	TOTAL CATIONS (µg/g)	% GRAVEL	% SAND		% SILT+CLAY	% CLAY
5	8.2	27.3	16.9	1440	244.2	1728.4	0.0	99.1	0.9	0.2	9.999
35	8.0	23.6	8.8	943	193.2	1168.6	0.0	99.9	0.1	0.0	0.170
35 ('81)	7.8	36.5	28.4	1503	204.1	1772.0	0.0	96.3	3.7	5.0	0.615
50	8.1	19.6	10.5	1216	233.3	1479.4	0.0	99.9	0.1	0.0	9.999
75	8.0	10.5	8.1	1198	202.3	1418.9	0.0	100.0	0.1	0.0	9.999
100	8.6	13.2	9.1	989	202.3	1213.6	0.0	99.9	0.1	0.0	9.999
150	8.4	25.0	11.5	1230	191.4	1457.9	0.0	100.1	0.1	0.0	9.999
AVG	8.2	19.9	10.8	1169	211.1	1410.8	0.0	99.8	0.2	0.0	9.999

1984 GRAND CANYON RIPARIAN ZONE EDAPHIC DATA

MILE/SIDE (SITE#): 43.1L (8) COLLECTION DATE 14-VIII-84 REACH TYPE: Large Eddy STAGE: ca. 1000m³/s

COVER TYPE(1981): Salix-Mixed COVER TYPE (1984): Open Beach

PROFILE: 0-100cm unstratified, moderately fine sand
100cm water

This site was scoured and then returned in 1983. No roots were encountered.

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE CHEMISTRY					TOTAL CATIONS (μg/g)	SUBSTRATE TEXTURE				% ORGANIC + CARBONATES
	pH	Na ⁺ (μg/g)	K ⁺ (μg/g)	Ca ⁺² (μg/g)	Mg ⁺² (μg/g)		% GRAVEL	% SAND	% SILT+CLAY	% CLAY	
5	8.4	20.3	13.2	1239	189.5	1462.0	0.0	98.7	1.3	0.4	9.999
35	8.3	11.5	8.8	1084	189.5	1293.8	0.0	100.0	0.1	0.0	0.171
(81)35	8.0	44.9	35.1	1576	196.8	1852.8	0.0	72.3	27.7	5.0	1.050
50	8.2	11.1	8.1	829	153.1	1001.3	0.0	100.0	0.1	0.0	9.999
75	8.3	23.3	13.8	1103	167.7	1307.8	0.0	99.7	0.3	0.4	9.999
100	8.0	21.5	14.2	1298	187.9	1521.6	0.0	98.4	1.5	1.4	9.999
AVG	8.2	17.5	11.6	1111	177.5	1317.6	0.0	99.4	0.7	0.4	9.999

1984 GRAND CANYON RIPARIAN ZONE EDAPHIC DATA

MILE/SIDE (SITE#): 43.2L (9) COLLECTION DATE 14-VIII-84 REACH TYPE: Large Eddy STAGE: ca. 1000m³/s
COVER TYPE(1981): Open Beach COVER TYPE (1984): Open Beach

PROFILE: 0-140cm unstratified, moderately fine sand
140cm water

This site was inundated in 1983. No roots were encountered.

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE CHEMISTRY				SUBSTRATE TEXTURE			
	pH	Na ⁺ (µg/g)	K ⁺ (µg/g)	Ca ²⁺ (µg/g)	Mg ²⁺ (µg/g)	TOTAL CATIONS (µg/g)	% GRAVEL	% SAND
5	8.0	16.2	6.8	948	129.4	1100.4	0.0	99.6
35	8.2	10.8	8.1	925	178.6	1122.5	0.0	99.9
(81)35	8.0	21.9	16.5	1358	187.7	1584.1	0.0	96.2
50	8.5	10.8	6.8	1007	142.1	1166.7	0.0	99.8
75	8.4	14.5	7.1	902	145.8	1069.4	0.0	99.8
100	8.3	13.2	8.1	1248	140.3	1409.6	0.0	100.2
145	8.4	17.5	9.1	1036	145.8	1208.4	0.0	99.8
AVG	8.3	13.8	7.7	1011	147.0	1179.5	0.0	99.9
							% SILT+CLAY	% CLAY
							0.4	0.0
							0.1	0.0
							3.8	3.5
							0.2	0.0
							0.1	0.2
							0.0	0.2
							0.1	0.0
							0.2	0.1
								% ORGANIC + CARBONATES
								9.999
								0.160
								1.884
								9.999
								9.999
								9.999
								9.999
								9.999
								9.999

MILE/SIDE (SITE#): 43.3L (10) COLLECTION DATE 24-VI-84 REACH TYPE: Large Eddy STAGE: ca. 350m³/s
COVER TYPE(1981): Prosopis COVER TYPE (1984): Prosopis

PROFILE:	0-10cm	10-125cm	125-130cm	130-150cm
	mixed organic and fine sand	fine sand	fine gravel and red silty sand (flash flood?)	red silty sand

Large roots to 125cm.
This site was not inundated in 1983.

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE CHEMISTRY					TOTAL CATIONS ($\mu\text{g/g}$)	SUBSTRATE TEXTURE				% ORGANIC + CARBONATES
	pH	Na^+ ($\mu\text{g/g}$)	K^+ ($\mu\text{g/g}$)	Ca^{+2} ($\mu\text{g/g}$)	Mg^{+2} ($\mu\text{g/g}$)		% GRAVEL	% SAND	% SILT+CLAY	% CLAY	
5	7.6	13.5	183.6	1891	233.3	2321.4	0.0	70.0	30.0	0.0	9.999
35	8.2	26.0	176.2	1781	271.5	2254.7	0.0	76.3	23.8	0.0	1.310
1)35	7.9	18.0	125.6	1549	162.2	1854.8	0.0	66.0	34.0	0.5	1.659
50	7.8	26.0	231.9	1544	226.0	2027.9	0.0	65.5	34.5	1.6	9.999
75	8.0	70.9	175.5	1399	490.2	2135.6	0.0	73.3	26.7	3.0	9.999
100	8.0	70.9	198.1	1535	388.4	2192.4	0.0	67.5	32.5	2.4	9.999
150	8.2	65.1	161.4	1868	421.0	2515.5	0.0	62.3	37.7	1.4	9.999
AVG	8.0	45.4	187.8	1670	338.4	2241.6	0.0	69.2	30.9	1.4	9.999

1984 GRAND CANYON RIPARIAN ZONE EDAPHIC DATA

MILE/SIDE (SITE#): 43.5L (11) COLLECTION DATE 20-X-84 REACH TYPE: Medium Eddy STAGE: 1100m³/s

COVER TYPE(1981): Dense Tamarix COVER TYPE (1984): Moderate Tamarix

PROFILE: 0-5cm brown silt
 5-30cm red sandy silt
 30-32cm brown silt
 32-72cm fine sand
 72-75cm black organic debris (buried duff layer)
 75-95cm brown silt
 95-97cm black organic layer
 97-125cm fine sand
 125-150 brown silt

Roots through 150cm depth, especially in upper 75cm. This site was inundated in 1983.
 PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE CHEMISTRY					SUBSTRATE TEXTURE				% ORGANIC + CARBONATES	
	pH	Na ⁺ (μg/g)	K ⁺ (μg/g)	Ca ⁺² (μg/g)	Mg ⁺² (μg/g)	TOTAL CATIONS (μg/g)	% GRAVEL	% SAND	% SILT+CLAY		% CLAY
5	8.1	23.6	24.0	1490	211.4	1749.0	0.0	88.3	11.6	1.6	9.999
35	7.9	20.9	10.8	1153	175.0	1359.7	0.0	94.9	5.2	0.0	0.220
('81)35	7.9	63.1	40.5	1449	184.1	1736.7	0.0	49.3	50.7	3.6	1.125
50	8.2	23.6	12.8	1066	184.1	1286.5	0.0	99.9	0.2	0.0	9.999
75	7.6	109.0	52.3	1380	353.5	1894.8	0.0	99.9	99.9	99.9	9.999
100	7.8	12.3	20.3	1039	122.1	1193.7	0.0	99.7	0.4	0.0	9.999
150	8.4	51.0	131.6	1230	185.9	1598.5	0.0	53.1	46.9	2.4	9.999
AVG	8.0	40.1	42.0	1226	205.3	1513.4	0.0	87.2	12.9	0.8	9.999

1984 GRAND CANYON RIPARIAN ZONE EDAPHIC DATA

MILE/SIDE (SITE#): 50.2L (13) COLLECTION DATE 21-X-84 REACH TYPE: Large Eddy STAGE: ca. 570m³/s

COVER TYPE(1981): Dense Salix COVER TYPE (1984): Open Beach

PROFILE: 0-150cm slightly cross-bedded, moderately fine sand

No roots encountered to 150cm.

This site was inundated in 1983, and has been deflated ca. 75cm or more.

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE CHEMISTRY					SUBSTRATE TEXTURE				
	PH	Na ⁺ (μg/g)	K ⁺ (μg/g)	Ca ²⁺ (μg/g)	Mg ²⁺ (μg/g)	TOTAL CATIONS (μg/g)	% GRAVEL	% SAND	% SILT+CLAY	% CLAY
5	8.2	24.3	11.1	1239	242.4	1516.8	0.0	99.2	0.8	0.0
35	8.2	17.9	16.9	1526	233.3	1794.1	0.0	96.8	3.1	0.0
(81)35	8.0	47.9	28.0	1531	236.9	1843.8	0.0	58.1	42.0	4.9
50	8.3	14.9	8.1	1057	173.1	1253.1	0.0	99.9	0.0	0.0
75	8.2	19.2	7.8	1071	195.0	1293.0	0.0	99.9	0.1	0.4
100	8.4	11.8	10.8	1276	200.5	1499.1	0.0	100.0	0.0	0.0
150	8.5	11.5	7.1	1007	171.3	1196.9	0.0	99.9	0.1	0.0
AVG	8.3	16.6	10.3	1196	202.6	1425.5	0.0	99.3	0.7	0.1
										% ORGANIC + CARBONATES
										9.999
										0.296
										1.146
										9.999
										9.999
										9.999
										9.999
										9.999

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DEPTH (cm)	SUBSTRATE CHEMISTRY					SUBSTRATE TEXTURE				% ORGANIC + CARBONATES	
	PH	Na ⁺ (μg/g)	K ⁺ (μg/g)	Ca ⁺² (μg/g)	Mg ⁺² (μg/g)	TOTAL CATIONS (μg/g)	% GRAVEL	% SAND	% SILT+CLAY		% CLAY
5	8.2	16.9	14.2	1194	173.1	1398.2	0.0	98.4	1.7	0.2	9.999
35	8.2	20.9	16.9	1294	165.8	1497.6	0.0	97.0	3.0	0.2	0.488
(81)35	8.1	10.5	29.0	1590	151.3	1780.8	0.0	95.8	4.3	99.9	0.305
50	8.1	50.0	42.5	1462	222.3	1776.8	0.0	72.0	27.9	1.2	9.999
75	8.2	92.2	61.1	1513	287.9	1954.2	0.0	56.7	43.3	5.2	9.999
100	8.3	632.4	58.1	1367	473.8	2531.3	0.0	41.7	58.3	4.4	9.999
AVG	8.2	162.5	38.6	1366	264.9	1832.0	0.0	73.2	26.8	2.4	9.999

1984 GRAND CANYON RIPARIAN ZONE EDAPHIC DATA

MILE/SIDE (SITE#): 94.9L (16) COLLECTION DATE 19-VIII-84 REACH TYPE: Straight STAGE: ca. 1700m³/s
 COVER TYPE(1981): Open Beach COVER TYPE (1984): Open Beach

PROFILE: 0-150cm silty sand with some bedding
 150cm rock

Roots to 150cm (Salix runners near surface with leaves).
 This site was inundated in 1983.

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE CHEMISTRY					SUBSTRATE TEXTURE					
	pH	Na ⁺ (μg/g)	K ⁺ (μg/g)	Ca ⁺² (μg/g)	Mg ⁺² (μg/g)	TOTAL CATIONS (μg/g)	% GRAVEL	% SAND	% SILT+CLAY	% CLAY	% ORGANIC + CARBONATES
5	8.4	17.6	17.9	1485	200.5	1721.0	0.0	95.7	4.4	0.0	9.999
35	8.1	17.6	16.9	1289	182.2	1505.7	0.0	94.6	5.4	0.0	0.307
() 35	8.1	10.1	32.1	1544	151.3	1737.5	0.0	96.6	3.4	99.9	0.554
50	8.1	13.8	15.5	1449	191.4	1669.7	0.0	97.3	2.7	99.9	9.999
75	8.2	24.0	16.5	1435	191.4	1666.9	0.0	97.3	2.7	2.0	9.999
100	8.0	16.9	18.2	1380	171.3	1586.4	0.0	96.4	3.5	0.8	9.999
150	8.1	32.7	27.0	1399	202.3	1661.0	0.0	84.7	15.3	7.4	9.999
AVG	8.2	20.4	18.7	1406	189.9	1635.0	0.0	94.3	5.7	2.0	9.999

1984 GRAND CANYON RIPARIAN ZONE EDAPHIC DATA

MILE/SIDE (SITE#): 122.2R (17) COLLECTION DATE 20-VIII-84 REACH TYPE: Mod. Eddy STAGE: ca. 1100m³/s

COVER TYPE(1981): Salix exigua COVER TYPE (1984): Open Beach

PROFILE: 0-70cm silty sand
70-90cm slightly bedded sandy silt
90-140cm silty sand
140cm water

No roots encountered.
This site was inundated in 1983.

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE CHEMISTRY					SUBSTRATE TEXTURE				% ORGANIC + CARBONATES	
	PH	Na ⁺ (μg/g)	K ⁺ (μg/g)	Ca ⁺² (μg/g)	Mg ⁺² (μg/g)	TOTAL CATIONS (μg/g)	% GRAVEL	% SAND	% SILT+CLAY		% CLAY
5	8.3	9.5	12.2	1221	160.4	1403.1	0.0	98.3	1.7	0.0	9.999
35	8.2	19.6	13.8	1062	136.7	1232.1	0.0	99.2	0.8	1.6	0.280
(^{'81}) 35	8.3	158.7	45.6	1390	309.8	1904.1	0.0	59.8	40.3	0.7	1.342
50	8.3	16.5	17.6	1394	169.5	1597.6	0.0	94.8	5.3	1.8	9.999
75	8.3	31.4	25.7	1554	189.5	1800.6	0.0	94.8	5.1	1.4	9.999
100	8.2	27.7	28.0	1522	178.6	1756.3	0.0	85.2	14.8	0.4	9.999
150	8.2	54.0	44.2	1449	293.4	1840.6	0.0	75.6	24.4	0.0	9.999
AVG	8.3	26.5	23.6	1367	188.0	1605.1	0.0	91.3	8.7	0.9	9.999

1984 GRAND CANYON RIPARIAN ZONE EDAPHIC DATA

MILE/SIDE (SITE#): 165.OR (18) COLLECTION DATE 24-VIII-84 REACH TYPE: Small Eddy STAGE: 850m³/s

COVER TYPE(1981): Sparse Tamarix COVER TYPE (1984): Open Beach

PROFILE: 0-2cm red sandy silt (from nearby tributary flood)

2-8cm silty sand

8-12cm red sandy silt

12-50cm silty sand

50cm water

No roots encountered at this site.
This site was inundated in 1983.

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE CHEMISTRY				SUBSTRATE TEXTURE			
	pH	Na ⁺ (µg/g)	K ⁺ (µg/g)	Ca ⁺² (µg/g)	Mg ⁺² (µg/g)	TOTAL CATIONS (µg/g)	% GRAVEL	% SAND
5	8.3	60.4	41.2	1868	233.3	2202.9	0.0	59.8
35	8.4	32.1	23.6	1549	213.2	1817.9	0.0	82.4
(1981) 35	8.0	73.9	56.7	1390	224.2	1744.8	0.0	71.4
50	8.4	30.7	17.6	1467	189.5	1704.8	0.0	96.6
AVG	8.4	41.1	27.5	1628	212.0	1908.6	0.0	79.6
							% CLAY	% SILT+CLAY
							2.2	40.1
							0.2	17.6
							1.8	28.6
							0.0	3.5
							0.8	20.4
							% ORGANIC + CARBONATES	
							9.999	
							0.662	
							0.869	
							9.999	
							9.999	

1984 GRAND CANYON RIPARIAN ZONE EDAPHIC DATA

MILE/SIDE (SITE#): 169.5R (19) COLLECTION DATE 1-VII-84 REACH TYPE: Straight STAGE: ca. 3600m³/s

COVER TYPE(1981): Dense Tamarix COVER TYPE (1984): Dense Tamarix

PROFILE: 0-150cm silty sand with minor bedding

Roots all through this pit.

This site was not inundated in 1983.

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE CHEMISTRY				SUBSTRATE TEXTURE						
	pH	Na ⁺ (μg/g)	K ⁺ (μg/g)	Ca ⁺² (μg/g)	Mg ⁺² (μg/g)	TOTAL CATIONS (μg/g)	% GRAVEL	% SAND	% SILT+CLAY	% CLAY	% ORGANIC + CARBONATES
5	8.4	147.8	206.6	1777	267.9	2399.3	0.0	29.3	70.6	5.8	9.999
35	8.1	235.1	115.4	1563	269.7	2183.2	0.0	35.6	64.4	2.8	2.927
('81) 35	7.8	81.0	74.6	1544	242.4	1942.0	0.0	67.4	32.7	2.4	1.414
50	8.2	408.2	29.4	1558	360.8	2356.4	0.0	26.9	73.0	99.9	9.999
75	8.2	461.1	30.0	1690	289.8	2470.9	0.0	27.7	72.2	2.6	9.999
100	8.2	798.2	53.7	1900	473.8	3225.7	0.0	18.6	81.3	3.8	9.999
150	8.2	634.2	29.0	1567	428.3	2658.5	0.0	41.7	58.3	4.0	9.999
AVG	8.2	447.4	77.4	1676	348.4	2549.2	0.0	30.0	70.0	3.8	9.999

MILE/SIDE (SITE#): 198.5R (20) COLLECTION DATE 25-VIII-84 REACH TYPE: Large Eddy STAGE: ca. 3700m³/s

COVER TYPE(1981): Acacia-Larrea COVER TYPE (1984): Acacia-Larrea

PROFILE:	2-0cm	0-5cm	5-6cm	2-23cm	23-27cm	27-50cm	50-53cm	87-97cm	97-100cm	100-150cm	red sandy silt	white clay	red silty sand (lensing out towards river.	Roots in upper 50cm.	This site was not inundated in 1983.
	duff	silty sand	red sandy silt	silty sand with some white clay	red sandy silt	silty sand with some white clay	sandy silt								

PHYSICAL AND CHEMICAL CHARACTERISTICS:

DEPTH (cm)	SUBSTRATE CHEMISTRY					SUBSTRATE TEXTURE					% ORGANIC + CARBONATES
	pH	Na ⁺ (μg/g)	K ⁺ (μg/g)	Ca ⁺² (μg/g)	Mg ⁺² (μg/g)	TOTAL CATIONS (μg/g)	% GRAVEL	% SAND	% SILT+CLAY	% CLAY	
5	9.9	6.4	155.3	1563	182.2	1906.9	0.0	45.1	55.0	3.0	9.999
35	8.1	43.5	78.0	1376	293.4	1790.9	0.0	47.6	52.3	16.4	2.648
50	8.1	51.3	48.9	1645	264.2	2009.4	0.0	14.9	85.2	9.4	9.999
75	7.7	168.1	72.6	1781	468.4	2490.1	0.0	50.4	49.7	1.0	9.999
100	8.3	16.9	40.8	1472	160.4	1690.1	0.0	81.9	18.2	0.4	9.999
150	8.0	83.4	121.5	1531	313.5	2049.4	0.0	47.6	52.5	15.0	9.999
AVG	8.0	61.6	86.2	1561	280.4	1989.2	0.0	47.9	52.2	7.5	9.999

APPENDIX 3.1: PLANT MORTALITY DATA FROM QUADRATS IN 1984.

SECTION	SPECIES
1 - Glen Cyn Dam to Lees Ferry	1 - <u>Tamarix chinensis</u>
2 - Mile 0 to Mile 61	2 - <u>Salix exigua</u>
3 - Mile 61 to 88	3 - <u>Tessaria sericea</u>
4 - Mile 88 to 166.5	4 - <u>Baccharis salicifolia</u> +
5 - Mile 166.5 to 226	<u>B. emoryi</u>
REACH TYPE	5 - <u>Baccharis sarothroides</u>
1 - Eddy	6 - <u>Baccharis sergiloides</u>
2 - Straight reaches	7 - <u>Prosopis glandulosa</u>
3 - Riffle	8 - <u>Acacia greggii</u>
4 - Rapid	9 - <u>Brickellia longifolia</u>
FLOODSTAGE	10 - <u>Aplopappus acradenius</u>
1 - ZONE A	11 - <u>Aster spinosus</u>
2 - ZONE B	12 - <u>Gutierrezia</u> spp.
3 - ZONE C	13 - Other riparian species
	14 - Other talus slope species
SUBSTRATE TYPE	
1 - Silt	
2 - Sand	
3 - Cobble	
4 - Mixed sand and cobble	
5 - Bedrock	
HEIGHT CLASS	
1 - Seedling	
2 - 0.0m to 1.0m	
3 - 1.0m to 2.0m	
4 - 2.0m to 3.0m	
5 - >3.0m	

APPENDIX 3.2:
ADDITIONAL SOURCES OF FLOOD-INDUCED PLANT MORTALITY
FROM GRAND CANYON, 1984

APPENDIX 3.2A1: MEAN STEM DENSITY/M² ON SIX 300M² SALIX EXIGUA STUDY PLOTS BEFORE AND AFTER INUNDATION.

RIVER MILE	YEAR	N	NO. LIVE STEMS/m ²	NO. DAMAGED STEMS/m ²	NO. DEAD STEMS/m ²	TOTAL % MORTALITY	TOTAL NO. STEMS/m ²	TOTAL % REMOVED 1982-1985
43.2L	1982	17	—	—	0.058	0.94	6.118	100
	1984		0.000	0.000	0.000	100	0.000	
50.2R	1982	26	—	—	0.803	21.96	4.460	-9.42
	1984-85		—	—	0.910	18.65	4.880	
64.0L	1982	13	—	—	0.583	9.57	6.090	100
	1984		0.000	0.000	0.000	100	0.000	
122.1R	1982	21	—	—	0.107	1.79	5.961	100
	1984		0.000	0.000	0.000	100	0.000	
123.0L	1982	14	—	—	0.453	3.51	12.867	100
	1984		0.000	0.000	0.000	100	0.000	
172.5L	1982	28	—	—	0.968	12.10	8.000	100
	1984		0.000	0.000	0.000	100	0.000	

- 1 Study plot size reduced from 300m² in 1982 to 140m² in 1985, a 53% loss of surface area.
2 Estimated with nearest neighbor distance equation: Density = $1/4r^2$ (Southwood, 1979), where $r =$
3 Study plot size = 1070m².

APPENDIX 3.2A2: ABSOLUTE STEM DENSITIES IN 3 TAMARIX CHINENSIS 10M x 30M STUDY PLOTS BEFORE AND AFTER INUNDATION.

RIVER MILE	YEAR	NO. LIVE STEMS	NO. DAMAGED STEMS	TAMARIX SEEDLING ₂ DENSITY/M ²	NO. DEAD STEMS	TOTAL % MORTALITY	TOTAL NO. OF STEMS	TOTAL % REMOVED 1982 - 85
43.5L	1982		246	0	130	34.57	376	
	1984	--	--	330	--	--	--	
	1985	141	83		113	33.53	337	10.37%
48.4R	1982		647	0	497	43.44	1144	
	1984	--	--	4.5	--	--	--	
	1985	202	152	0.05	168	32.18	522	54.37%
169.5R	1982		87	0	73	45.63	160	
	1985	27	46	46	55	42.97	128	20.00%

APPENDIX 3.2B: PERCENT REMOVAL, PERCENT DROWNED, AND TOTAL PERCENT MORTALITY OF INDIVIDUAL PLANTS UNDER OBSERVATION IN ZONES A AND B, 1980-1984.

<u>SPECIES</u>	<u>%REMOVED</u>	<u>%DROWNED</u>	<u>TOTAL %MORTALITY (n)</u>
Tach	28.82	34.65	49.41 (170)
Saex (clones)	14.93	0.00	14.93 (68)
Tese (clones)	33.33	20.00	44.44 (18)
Basp	54.55	22.73	77.27 (44)
Acgr	0.00	50.00	50.00 (6)
Prgl	14.29	42.86	57.33 (14)
	---	44.74	44.74 (76)
Phau (clones)	42.31	0.00	42.31 (26)
Tyla (clones)	83.33	0.00	83.33 (12)
<u>Scirpus</u> (clones)	100.00	0.00	100.00 (2)
Sago	6.67	7.14	13.33 (15)

APPENDIX 3.2C : SOURCES OF FLOOD-INDUCED REMOVAL AND DROWNING
MORTALITY DATA FROM "FLOATING TRANSECTS"

<u>MILE AND SIDE</u>	<u>DATE CENSUSED</u>	<u>SPECIES & MORTALITY (n)</u>
45.5-46.8R	September, 1983	Basp 79.72 (286) m
54-56R (1010m)	August, 1982	Tach 5.76 (260) m
		Saex 0.00 (842) m
		Basp 0.00 (416) m
		Prgl 0.00 (4) m
60.0-61.0L	October, 1982	Tach 0.00 (941) r,m
		Saex 0.00 (12,000) r,m
		Basp 0.00 (434) r,m
		Prgl 0.00 (6) r,m
	August, 1984	Tach 16.20 (748) r,m
		Saex 2.06 (3952) r,m
		Basp 98.70 (76) r,m
		Prgl 83.30 (6) r,m
79.0-80.0R+L	October, 1983	Tach 27.27 (55) m
97.5-98.0R	August, 1984	Basp 45.61 (57) m
155-157R+L	August, 1984	Tach 93.10 (87) m
165.0L	August, 1984	Basr 79.53 (127) m
166.5-179.5R	October, 1981	Prgl 0.00 (36) r,m
	July, 1984	Prgl 59.70 (67) r,m
	July, 1985	Prgl 54.69 (64) r,m
180-225,5R+L	August, 1984	Prgl 56.63 (83) m
196.5-198.2R	October, 1982	Tach 0.00 (1800) r,m
		Saex 0.00 (1 clone) r,m
		Tese 0.00(14 clones)r,m
		Basp 0.00 (17) r,m
		Basr 0.00 (1004) r,m
		Prgl 0.00 (36) r,m
		Phau 0.00 (3 clones) r,m

<u>MILE AND SIDE</u>	<u>DATE CENSUSED</u>	<u>SPECIES & MORTALITY (n)</u>
196.5-198.2 (contiued)	August, 1984	Tach 6.85 (1389) r,m Saex 0.00 (0) r,m Tese 0.00 (13) r,m Basp 0.00 (1) r,m Basr 56.78 (796) r,m Prgl 27.50 (40) r,m Phau 0.00 (2) r,m
217-224L+R*	August, 1984	Acgr 4.09 (109) m
223.8-225.4L+R	August, 1984	Prgl 38.89 (18) m

* Zone D only

r = data used to calculate %mortality due to removal.

m = data used to calculate %mortality due to drowning.

APPENDIX 3. 2D : MORTALITY BY PLANT SPECIES ON COBBLE BARS
AND COBBLE ISLANDS

<u>MILE AND SIDE</u>	<u>DATE CENSUSED</u>	<u>SPECIES & MORTALITY (n)</u>
53.3R Cbl. Is.	August, 1982	Tach 0.00 (184)
		Basp 0.00 (14)
	September	Tach 98.46 (65) r,m
		Basp 0.00 (0) all remvd
56.6R Cbl. Bar	August, 1984	Tach 79.42 (379) m
61.0R Cbl. Is.	June, 1984	Tach 87.50 (8) m
61.0L Cbl. Is.	June, 1984	Tach 96.82 (157) m
73.0R Cbl. Is.	May, 1983	Tach 0.00 (150) r,m
	September, 1983	Tach 88.89 (90) r,m
73.1L Cbl. Bar	September, 1983	Tach 90.00 (100) m
88.5L Cbl. Is.	August, 1984	Tach 100.00 (48) m

r = data used to calculate %mortality due to removal.

m = data used to calculate %mortality due to drowning.

APPENDIX 3.2E: AERIAL PHOTOGRAPH ANALYSES OF TAMARIX CHINENSIS
 MORTALITY DUE TO REMOVAL AND DROWNING IN
 STRAIGHT REACHES¹, COBBLE BARS², AND RAPIDS³
 IN GRAND CANYON, 1984.

%REMOVAL, %DROWNED AND			
<u>MILE, SIDE</u>	<u>PHOTO DATE</u>	<u>CENSUS DATE</u>	<u>TOTAL %MORTALITY (n)</u>
72.0R ¹	November, 1980	August, 1984	0.00, 37.50, 37.50 (16)
73.0R ²	November, 1980	August, 1984	0.00, 2.63, 2.63 (38)
76.3L ³	November, 1982	August, 1984	22.22, 71.43, 77.78 (36)
76.4L ²	November, 1982	August, 1984	0.00, 26.09, 26.09 (46)
94.8R ²	November, 1980	August, 1984	90.00, 100.0, 100.0 (10)
98.0R	November, 1980	August, 1984	11.90, 13.51, 23.81 (42)
125.0R ²	May, 1981	August, 1984	0.00, 35.00, 35.00 (40)
133.5L ¹	November, 1980	August, 1984	0.00, 0.00, 0.00 (5)
133.6L ³	November, 1980	August, 1984	0.00, 100.0, 100.0 (4)
	* *	* *	* *

MORTALITY BY REACH TYPE

Straight Reaches	0.00%R,	28.57%M,	28.57% Total Mortality	(21)
Riffles	6.72%R,	22.40%M,	27.61% Total Mortality	(134)
Rapids	15.85%R,	42.03%M,	51.22% Total Mortality	(82)

APPENDIX 3.3:
COMMON PLANTS OF THE COLORADO RIVER RIPARIAN ZONE, 1984.

Families

Anacardiaceae

Rhus trilobata Nutt.

squaw-bush

location: Ca. mile 37.5 L, above Marble Canyon drill sites at the bend of River.

Date: 14-VIII-84. Coll: A. Neas Elev: ca. 3150'

Asclepidaceae

Asclepias latifolia (Torr.) Raf.

milkweed

location: Mile 24.5 L, along River below camp, common.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

Sarcostemma cynanchoides Decne.

climbing milkweed

location: Mile 50 L near camp.

Date: 16-VIII-84. Coll: A. Neas Elev: ca. 2850'

Asteraceae

Artemesia filifolia Torr.

location: Near mile 11 R, Soap Creek Rapid on beach.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3075'

Artemesia ludoviciana Nutt. ssp. albula (Woot.) Keck.

location: Mile 8 R, beach at Badger Creek Rapid, common.

Date: 12-VIII-84. Coll: A. Neas Elev: ca. 3150'

Artemesia ludoviciana Nutt. var. mexicana (Wind.) Keck.

location: Mile 24.5 L, along River at camp, common.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

Aster spinosus Benth.

spiny aster

location: Mile 9.5 L, at Steven's study plot on slope.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

location: Mile 24.5 L, along River at camp, common.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

Baccharis glutinosa Pers.

seep-willow

location: Mile ca. 53 R, near camp below Nankoweap Rapid.

Date: 16-VIII-84. Coll: A. Neas Elev: ca. 2775'

Brickellia longifolia Wats.

location: Mile 8 R, beach at Badger Creek Rapid, common.

Date: 12-VIII-84. Coll: A. Neas Elev: ca. 3150'

Chrysothamnus nauseosus (Pall) Britton rabbitbrush

location: Near mile 11 Soap Creek, on beach at bottom of slope.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3075'

Conyza canadensis (L.) Cronquist horseweed

location: Mile 8 R, beach at Badger Creek Rapid, common.

Date: 12-VIII-84. Coll: A. Neas Elev: ca. 3150'

Dicortia sp.

location: Mile ca. 32 R, at sandbar above Vasey's Paradise.

Date: 14-VIII-84. Coll: A. Neas Elev: ca. 2875'

Remarks: Collect plants in fruit, in September.

Dyssodia thurberi (Gray) Robins. dogweed

location: Mile 9.5 L, at Steven's study plot on slope.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

location: Mile 24.5 L, along slope above camp, common.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

location: Ca. mile 71.3 R, beach below Cardenas Creek.

Date: 18-VIII-84. Coll: A. Neas Elev: ca. 2750'

Gnaphalium cf. chilense Spreng

location: Mile ca. 53 R near camp below Nankoweap Rapid.

Date: 16-VIII-84. Coll: A. Neas Elev: ca. 2775'

Gutierrezia microcephala (DC) Gray snake-weed

location: Mile 8 R, beach at Badger Creek Rapid, common.

Date: 12-VIII-84. Coll: A. Neas Elev: ca. 3150'

Iva acerosa (Nutt.) Jackson copperweed

location: Mile 98 R ca. 0.25 mile from Crystal Creek.

Date: 20-VIII-84. Coll: L. Stevens Elev: ca. 2400'

Remarks: Only one specimen was collected; collect more for NAU.

Leucelene ericoides (Torr.) Greene

location: Mile 24.5 L, along slope above camp, very common.
 Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

Perityle emoryi Torr.

rock daisy

location: Mile 65.3 R side of River above Lava Canyon Rapid.
 Date: 17-VIII-84. Coll: A. Neas Elev: ca. 2695'
 Remarks: Collect more for NAU.

Plurocoronis pluriseta (Gray) R. King & H. Robinson

location: Mile 144 R side of River.
 Date: 23-VIII-84. Coll: L. Stevens Elev: ca. 1875'
 Remarks: Only one small specimen was collected; it was in poor shape; others need to be collected in flower and/or fruit.

Solidago occidentalis

goldenrod

location: Mile ca. 32 R at sandbar above Vasey's Paradise.
 Date: 14-VIII-84. Coll: A. Neas Elev: ca. 2875'
 Remarks: Common, mixed with Carex, and poison ivy.

Stephanemeria exigua Nutt.

location: Mile 8 R, beach at Badger Creek Rapid, common.
 Date: 12-VIII-84. Coll: A. Neas Elev: ca. 3150'

Tessaria sericea (Nutt.)

arrow weed

location: Mile 8 R, beach at Badger Creek Rapid, common.
 Date: 12-VIII-84. Coll: A. Neas Elev: ca. 3150'

location: Mile ca. 53 R near camp below Nankoweap Rapid.
 Date: 16-VIII-84. Coll: A. Neas Elev: ca. 2775'
 Remarks: A few plants were flowering.

Xylorhiza tortifolia (T. & G.) Greene

desert aster

location: Mile 9.5 L, at Steven's study plot on slope.
 Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'
 Remarks: Plant was without flowers; collect in flower, if possible.

Boraginaceae

Cryptantha sp.

location: Mile 24.5 L, along River below camp, common.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

Brassicaceae

Lepidium fremontii Wats.

peppergrass

location: Mile 8 R, beach at Badger Creek Rapid, common.

Date: 12-VIII-84. Coll: A. Neas Elev: ca. 3150'

location: Mile 9.5 L, at Steven's study plot on slope.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

Lepidium montanum Nutt.

peppergrass

location: Mile ca. 53 R near camp below Nankoweap Rapid.

Date: 16-VIII-84. Coll: A. Neas Elev: ca. 2775'

Remarks: Plants were flowering; collect large fruiting plants for NAU.

Stanleya pinnata (Pursh) Britton

desert plume

location: Mile 24.5 L, along River below camp, common.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

Chenopodiaceae

Corispermum nitidum Kit.

bug-seed

location: Mile 50.3 L, on beach at camp.

Date: 15-VIII-84. Coll: A. Neas Elev: ca. 3000'

location: Mile 179 L, above Lava Falls Rapid.

Date: 25-VIII-84. Coll: L. Stevens Elev: ca. 1700'

Suaeda torreyana Wats.

seepweed

location: Mile 52.5 R, beach near Nankoweap Rapid.

Date: 16-VIII-84. Coll: L. Stevens Elev: ca. 2775'

Cyperaceae

Carex sp.

sedge

location: Mile ca. 32 R at sandbar above Vasey's Paradise.

Date: 14-VIII-84. Coll: A. Neas Elev: ca. 2875'

Cyperus sp.

sedge

location: Mile 52.5 R, beach near Nankoweap Rapid.

Date: 16-VIII-84. Coll: A. Neas Elev: ca. 2775'

Scirpus validus Vahl.

bullrush

location: Mile 52.5 R, beach pond near Nankoweap Rapid camp.

Date: 16-VIII-84. Coll: A. Neas Elev: ca. 2775'

Ephedraceae

Ephedra torreyana Wats.

jointfir

location: Near mile 11 R, Soap Creek Rapid

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3075'

location: Mile 24.5 along River below camp on east side, common.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

Equisetaceae

Equisetum hyemale L.

scouring rush

location: Mile ca. 32 R at sandbar above Vasey's Paradise.

Date: 14-VIII-84. Coll: A. Neas Elev: ca. 2875'

Fabaceae

Amorpha fruticosa var. occidentalis (Abrams) Kearney & Peebles

False-indigo

location: Ca. mile 8 L, beach near Jackass Creek.

Date: 12-VIII-84. Coll: A. Neas Elev: ca. 3100'

Cassia covesii Gray

location: Ca. mile 71.3 R, beach below Cardenas Creek.

Date: 18-VIII-84. Coll: A. Neas Elev: ca. 2750'

Medicago sativa L.

alfalfa

location: Mile 52.5 R, beach near Nankoweap Rapid.

Date: 16-VIII-84. Coll: A. Neas Elev: ca. 2775'

Lamiaceae

Hedeoma diffusum Greene

Mock-pennyroyal

location: Mile 24.5 L, along River below camp, common.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

Loasaceae

Mentzelia pumila (Nutt.) Torr. & Gray

stickleaf

location: Mile ca. 43.8 L, on sandy area near camp, common.

Date: 15-VIII-84. Coll: A. Neas Elev: ca. 2850'

Malvaceae

- Sphaeralcea subulata? Coult. globe-mallow
 location: Mile ca. 71.3 R, on sandy area in camp, common.
 Date: 17-VIII-84. Coll: A. Neas Elev: ca. 2700'
 Remarks: Collect fruiting plants.

Nyctaginaceae

- Abronia fragrans Nutt. sand-verbena.
 location: Mile ca. 52.5 R, on sandy area below Nankoweap Rapid.
 Date: 17-VIII-84. Coll: A. Neas Elev: ca. 2775'
- location: Mile ca. 71.3 R, on sandy area in camp, common.
 Date: 17-VIII-84. Coll: A. Neas Elev: ca. 2700'

Onagraceae

- Oenothera pallida Lindl. evening primrose
 location: Mile 8 R, beach at camp, Badger Creek Rapid, common.
 Date: 12-VIII-84. Coll: A. Neas Elev: ca. 3150'

Plantaginaceae

- Plantago major L. plantain
 location: Mile ca. 32 R, at sandbar above Vasey's Paradise.
 Date: 14-VIII-84. Coll: A. Neas Elev: ca. 2875'
 Remarks: Likely to be a common weedy plant along beaches.

Poaceae

Agrostis semiverticillata (Forsk.) Christ

location: Mile ca. 32 R, at sandbar above Vasey's Paradise.

Date: 14-VIII-84. Coll: A. Neas Elev: ca. 2875'

location: Mile 52.5 R, beach at Nankoweap Rapid.

Date: 16-VIII-84. Coll: A. Neas Elev: ca. 2775'

Aristida wrightii Nash

three-awn

location: Mile 24.5 L, on slope above camp.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3175'

location: Mile ca. 32 R at sandbar above Vasey's Paradise.

Date: 14-VIII-84. Coll: A. Neas Elev: ca. 2875'

Bouteloua curtipendula (Michx.) Torr.

side-oats grama

location: Mile 52.5 R, beach at Nankoweap Rapid.

Date: 16-VIII-84. Coll: A. Neas Elev: ca. 2775'

Bromus tectorum L.

downy chess

location: Mile 24.5 L, on slope above camp.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3175'

Bromus willdenowii Kunth.

rescue grass

location: Mile 50 L near camp.

Date: 16-VIII-84. Coll: A. Neas Elev: ca. 2850'

Distichlis spicata (L.) Greene var. stricta (Gray) Beetle

saltgrass

location: Mile 24.5 L, along River below camp, common.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

Erioneuron pulchellum (H.B.K.) Tateoka.

fluffgrass

location: Mile 24.5 L, on slope above camp.

Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3175'

location: Ca. mile 71.3 R, beach below Cardenas Creek.

Date: 18-VIII-84. Coll: A. Neas Elev: ca. 2750'

Muhlenbergia porteri Scribn. bush muhly
 location: Mile 24.5 L, along River below camp, common.
 Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

Panicum capillare L.
 location: Mile 24.5 R, along River below camp, common.
 Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

Panicum obtusum H.B.K. vine mesquite
 location: Mile ca. 24.5 L, along River below camp, common.
 Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'

location: Mile 179.0 L along River below camp on east side.
 Date: 25-VIII-84. Coll: L. Stevens Elev: ca. 1750'
 Remarks: Trailing and growing in a straight column toward River.

Polypogon monspeliensis (L.) Desf. rabbitfoot grass
 location: Mile ca. 24.5 L, along River below camp, common.
 Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3175'

location: Ca. 50.2 L mile on beach at the camp.
 Date: 15-VIII-84. Coll: A. Neas Elev: ca. 2850'

location: Mile ca. 32 R at sandbar above Vasey's Paradise.
 Date: 14-VIII-84. Coll: A. Neas Elev: ca. 2875'

Schizachyrium scoparium (Michx.) Nash little bluestem
 location: Mile 8 R, beach at Badger Creek Rapid, common.
 Date: 12-VIII-84. Coll: A. Neas Elev: ca. 3150'

location: Mile 179 L, above Lava Falls Rapid.
 Date: 25-VIII-84. Coll: L. Stevens Elev: ca. 1700'

Sporobolus cryptanthus (Torr.) Gray sand dropseed
 location: Mile ca. 24.5 L, along River below camp, common.
 Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3175'

location: Ca. 50.2 L mile on beach at the camp.
 Date: 15-VIII-84. Coll: A. Neas Elev: ca. 2850'

Polygonaceae

Eriogonum microthecum (Torr.) Woot. & Stand. wild-buckwheat
 location: Mile ca. 52.5 R on sandy area below Nankoweap Rapid.
 Date: 17-VIII-84. Coll: A. Neas Elev: ca. 2775'

Polygonum coccineum Muhl. smartweed
 location: Mile ca. 32 R at Vasey's Paradise in wet area.
 Date: 14-VIII-84. Coll: A. Neas Elev: ca. 2875'
 Remarks: Growing with poison ivy, and Adiantum capillis-veneris.

Pteridaceae

Adiantum capillis-veneris L. venus-maidenhair fern
 location: Mile ca. 32 R at Vasey's Paradise in wet area.
 Date: 14-VIII-84. Coll: A. Neas Elev: ca. 2875'
 Remarks: Growing with poison ivy, common.

Rosaceae

Fallugia paradoxa (D. Don.) Endl. Apache plume
 location: Mile 24.5 L, in camp at bottom of slope.
 Date: 14-VIII-84. Coll: A. Neas Elev: ca. 3025'.

Salicaceae

Salix exigua Nutt. coyote willow
 location: Mile 8 R, at Badger Creek Rapid camp.
 Date: 12-VIII-84. Coll: A. Neas Elev: ca. 3150'.

location: Mile 133 site 2 up Tapeats Creek ca. 1.5 mi.
 Date: 21?-VIII-84. Coll: L. Stevens Elev: ca. 2350'.
 Remarks: Polymorphic; in flower.

Solanaceae

Lycium andersonii Gray wolfberry
 location: Mile ca. 24.5 L, along River below camp, common.
 Date: 13-VIII-84. Coll: A. Neas Elev: ca. 3150'.

Nicotiana trigonophylla Dunal. tobacco
 tobacco
 location: Mile ca. 32 R on sand bar above Vasey's Paradise.
 Date: 14-VIII-84. Coll: A. Neas Elev: ca. 2875'

Tamaricaceae

Tamarix pentandra Poll.

location: Mile 8 R, at Badger Creek Rapid camp.

Date: 12-VIII-84. Coll: A. Neas Elev: ca. 3150'

location: Mile 139 at Fishtail Sinks.

Date: 24-VIII-84. Coll: L. Stevens Elev: ca. 1950'

Verbenaceae

Phyla cuneifolia (Torrey) Greene

location: Mile ca. 52.5 R on sandy area below Nankoweap Rapid.

Date: 17-VIII-84. Coll: A. Neas Elev: ca. 2775'

APPENDIX 4.1:
INVERTEBRATE SWEEP-NET COLLECTION DATA BY GUILD FROM
THREE SALIX EXIGUA AND THREE TAMARIX CHINENSIS STUDY SITES
IN GRAND CANYON, 1980-1985.

SITE: S2 (MILE 50.2R). SALIX EXIGUA

DATE	N _H	S _H	B _H	J' _H	N _P (S _P)	B _P	N _{PA} (S _{PA})	B _{PA}	N _I (S _I)	B _I	N _{TOT} (S _{TOT})	B _{TOT}
13-III-80	--	--	0.1835	--	--	1.0195	--	0.0364	--	0.0242	--	1.2636
14-VI-80	180	20	0.1612	.699	23 (11)	0.1159	41 (29)	0.0006	142 (16)	0.0303	386 (76)	0.3080
19-VII-80	580	10	0.1135	.453	6 (3)	0.0929	45 (13)	0.0005	35 (4)	0.0204	666 (29)	0.2274
20-VIII-80	172	8	0.0678	.725	6 (4)	0.1774	29 (13)	0.0038	152 (8)	0.0267	359 (33)	0.2755
25-IX-80	105	12	0.0429	.696	11 (5)	0.0821	6 (4)	0.0000	18 (4)	0.0010	140 (25)	0.1261
29-X-80	72	7	0.1243	.623	2 (2)	0.1056	0 (0)	0.0003	12 (5)	0.0000	86 (14)	0.2302
21-VI-81	593	16	--	.536	28 (8)	--	70 (24)	--	221 (9)	--	912 (57)	--
20-V-82	81	15	--	.814	7 (5)	--	9 (7)	--	176 (9)	--	272 (35)	--
12-VIII-82	304	13	--	.632	26 (10)	--	8 (6)	--	388 (14)	--	726 (43)	--
18-X-82	267	15	--	.585	29 (7)	--	9 (7)	--	156 (15)	--	455 (45)	--
21-V-83	59	12	--	.698	20 (11)	--	32 (16)	--	228 (29)	--	339 (68)	--
16-VI-83	115	9	--	.832	13 (5)	--	4 (3)	--	107 (9)	--	239 (26)	--
23-IX-83	526	10	--	.640	17 (6)	--	10 (7)	--	41 (9)	--	594 (32)	--
24-VI-84	537	17	--	.631	29 (6)	--	11 (10)	--	136 (6)	--	713 (39)	--
25-VIII-84	199	14	--	.627	13 (5)	--	9 (3)	--	34 (4)	--	255 (26)	--
21-X-84	65	6	--	.818	9 (5)	--	1 (1)	--	275 (6)	--	350 (18)	--
4-VI-85	114	11	--	.679	12 (6)	--	32 (23)	--	355 (8)	--	513 (48)	--
23-VI-85	140	13	--	.592	9 (5)	--	16 (7)	--	96 (5)	--	261 (30)	--
26-VII-85	181	13	--	.518	13 (6)	--	11 (6)	--	126 (6)	--	331 (31)	--

SITE: T1 (MILE 43.5L): TAMARIX CHINENSIS

DATE	N _H	S _H	B _H	J' _H	N _P (S _P)	B _P	N _{PA} (S _{PA})	B _{PA}	N _I (S _I)	B _I	N _{TOT} (S _{TOT})	B _{TOT}
21-V-80	1035	8	3.4266	.045	25 (7)	0.1222	10 (8)	0.0000	15 (7)	0.0255	1085 (30)	3.5743
12-VI-80	121	1	4.3449	∞	6 (4)	0.1501	7 (4)	0.0001	2 (2)	0.0041	136 (11)	4.4992
18-VII-80	461	7	5.8710	.135	5 (2)	0.1562	14 (3)	0.0006	0 (0)	0.0463	480 (12)	6.0742
17-VIII-80	1111	4	13.5740	.099	16 (6)	0.3527	16 (1)	0.0001	12 (3)	0.0037	1155 (14)	13.9305
23-IX-80	223	2	1.2949	.244	35 (4)	0.8220	13 (1)	0.0007	4 (3)	0.0107	275 (10)	2.1283
27-X-80	183	3	1.5016	.086	15 (4)	0.2494	0 (0)	0.0014	29 (1)	0.0072	289 (8)	1.7596
18-V-81	19	1	--	∞	24 (3)	--	0 (0)	--	1303 (11)	--	1346 (15)	--
19-VI-81	19	1	0.0120	∞	16 (5)	0.0659	7 (5)	0.0019	55 (12)	0.0450	97 (23)	0.1248
17-X-81	498	5	--	.043	47 (6)	--	2 (2)	--	11 (9)	--	558 (22)	--
7-IV-82	2	2	--	1.000	12 (3)	--	1 (1)	--	36 (5)	--	51 (11)	--
13-VI-82	236	4	--	.059	4 (3)	--	1 (1)	--	22 (3)	--	263 (11)	--
20-V-82	514	4	--	.089	7 (4)	--	6 (4)	--	6 (2)	--	533 (14)	--
12-VIII-82	75	5	--	.291	25 (9)	--	1 (1)	--	15 (2)	--	116 (17)	--
16-X-82	5	4	--	.961	24 (5)	--	3 (2)	--	29 (6)	--	61 (17)	--
21-V-83	7	5	--	.917	13 (3)	--	12 (9)	--	29 (4)	--	61 (21)	--
22-IX-83	171	4	--	.078	5 (4)	--	2 (2)	--	10 (4)	--	188 (14)	--
31-V-84	196	2	--	.198	4 (3)	--	18 (2)	--	32 (5)	--	250 (12)	--
23-VI-84	277	6	--	.364	9 (5)	--	160 (3)	--	59 (6)	--	505 (20)	--
25-VII-84	3039	3	--	.098	27 (5)	--	11 (2)	--	24 (3)	--	3101 (13)	--
15-VIII-84	818	2	--	.233	32 (8)	--	272 (3)	--	21 (3)	--	1143 (16)	--
20-X-84	19	2	--	.486	12 (3)	--	0 (0)	--	72 (4)	--	103 (9)	--
25-VII-85	350	5	--	.131	24 (8)	--	4 (3)	--	395 (8)	--	773 (24)	--

SITE: T2 (MILE 48.4R). TAMARIX CHINENSIS

DATE	N _H	S _H	B _H	J' _H	N _p (S _p)	B _p	N _{PA} (S _{PA})	B _{PA}	N _I (S _I)	B _I	N _{TOT} (S _{TOT})	B _{TOT}
19-VII-80	697	4	2.5707	.041	23 (10)	0.0844	76 (1)	0.0032	1 (1)	0.0503	797 (16)	2.7086
20-VIII-80	2664	2	11.3281	.013	31 (4)	0.5319	17 (2)	0.0004	47 (3)	0.0603	2759 (11)	11.9206
24-IX-80	1172	5	9.2334	.052	26 (8)	0.7714	100 (2)	0.0001	23 (7)	0.0461	1327 (22)	10.0508
28-X-80	700	4	4.6336	.102	21 (7)	0.1383	30 (1)	0.0001	49 (3)	0.0418	800 (15)	4.8138
20-VI-81	44	2	--	.157	13 (5)	--	2 (2)	--	30 (4)	--	89 (13)	--
20-V-82	680	3	--	.058	13 (5)	--	5 (4)	--	61 (7)	--	759 (19)	--
12-VIII-82	344	3	--	.271	24 (7)	--	21 (2)	--	10 (3)	--	399 (15)	--
18-X-82	11	4	--	.683	27 (5)	--	5 (4)	--	43 (10)	--	87 (24)	--
21-V-83	2	2	--	1.000	15 (7)	--	8 (7)	--	28 (5)	--	53 (21)	--
23-IX-83	337	5	--	.107	16 (7)	--	0 (0)	--	12 (4)	--	365 (16)	--
24-VI-84	1154	3	--	.063	4 (3)	--	197 (2)	--	296 (4)	--	1651 (12)	--
25-VII-84	5187	5	--	.023	56 (6)	--	245 (3)	--	66 (3)	--	5554 (17)	--
16-VIII-84	42	3	--	.658	13 (5)	--	83 (4)	--	10 (2)	--	139 (13)	--
21-X-84	15	2	--	.353	17 (4)	--	1 (1)	--	260 (4)	--	293 (11)	--
4-VI-85	5	3	--	.590	5 (2)	--	2 (2)	--	99 (4)	--	111 (11)	--
23-VI-85	9	6	--	.861	6 (5)	--	2 (2)	--	402 (10)	--	419 (23)	--
26-VII-85	410	5	--	.229	9 (6)	--	3 (3)	--	79 (12)	--	501 (26)	--

SITE: T3 (MILE 169.5R) • TAMARIX CHINENSIS

DATE	N _H	S _H	B _H	J' _H	N _P (S _P)	B _P	N _{PA} (S _{PA})	B _{PA}	N _I (S _I)	B _I	N _{TOT} (S _{TOT})	B _{TOT}
20-III-80	--	--	0.0005	--	--	0.3217	--	0.0000	--	0.0651	--	0.3873
21-VI-80	36	4	1.7496	.273	2 (2)	0.0484	0 (0)	0.0013	1 (1)	0.0104	39 (7)	1.8096
27-VII-80	131	2	0.9879	.416	2 (1)	0.0679	2 (1)	0.0032	1 (1)	0.0180	136 (5)	1.0770
25-VIII-80	30	5	0.0797	.523	14 (6)	0.0593	1 (1)	0.0015	5 (3)	0.0026	50 (15)	0.1432
2-X-80	15	4	0.1639	.836	3 (2)	0.0264	0 (0)	0.0019	1 (1)	0.0042	19 (7)	0.1963
6-XI-80	4	1	0.3308	∞	2 (2)	0.0196	1 (1)	0.0005	7 (3)	0.0011	14 (7)	0.3519
27-VI-81	25	2	--	.402	20 (6)	--	2 (1)	--	79 (2)	--	126 (11)	--
26-X-81	22	4	--	.716	5 (3)	--	1 (1)	--	1 (1)	--	29 (9)	--
30-V-82	380	3	--	.059	2 (1)	--	1 (1)	--	2 (1)	--	385 (6)	--
21-VIII-82	37	3	--	.785	11 (8)	--	10 (6)	--	4 (4)	--	62 (21)	--
27-X-82	16	6	--	.804	5 (3)	--	2 (2)	--	9 (7)	--	32 (18)	--
30-V-83	25	5	--	.709	6 (5)	--	1 (1)	--	1 (1)	--	33 (12)	--
7-X-83	128	4	--	.529	9 (8)	--	1 (1)	--	7 (4)	--	145 (17)	--
8-VI-84	63	3	--	.202	3 (2)	--	26 (3)	--	9 (1)	--	101 (9)	--
4-VII-84	25	5	--	.730	8 (3)	--	6 (2)	--	29 (4)	--	68 (14)	--
1-VIII-84	27	2	--	.503	2 (2)	--	1 (1)	--	2 (2)	--	32 (7)	--
25-VIII-84	21	2	--	.276	4 (2)	--	1 (1)	--	2 (2)	--	28 (7)	--
2-VIII-85	12	3	--	.981	2 (2)	--	0 (0)	--	1 (1)	--	15 (6)	--

APPENDIX 4.2

A: SPECIES OF PHYTOPHAGOUS INVERTEBRATES COLLECTED FROM
SALIX EXIGUA IN GRAND CANYON.

B: SPECIES OF PHYTOPHAGOUS INVERTEBRATES COLLECTED FROM
TAMARIX CHINENSIS IN GRAND CANYON AND THE UNITED STATES

APPENDIX 3.2a: INVERTEBRATE HERBIVORES COLLECTED FROM
SALIX EXIGUA NUTT. IN THE GRAND CANYON, ARIZONA.

ACARINA

Acarina sp. 1

ORTHOPTERA

Gryllidae

Oecanthus quadripunctatus Beutenmuller 1

Locustidae

Melanoplus sp. 1

Schistocerca shoshoni Schudder 1

HOMOPTERA

Aphididae

Macrosiphum euphorbiae (Thomas) 1

Aphidid spp. I-IX

Cicadellidae

Aceratagallia sp. 1

Agalliopsis sp. 1

Alconeura unipuncta (Gillette) 1,2

Alconeura sp. I 1

Balclutha punctata (Fabricius) 1

Ceratagallia vastitatis (Oman) 2

"Dikraneura" sp. 1

Empoasca neaspersa Oman & Wheeler 1

Empoasca ophiopera Ross and Cunningham 1,2

Idiocerus rotundens Del & Cald 1,2

Idiocerus ramentosus (Uhler) 1,2

Idiocerus sp. I 1

Koebelia irrorata Ball 1

Opsius stactogalus Fieber 1,2

Cicadellid spp. I-VI 1

Cicadidae

Diceroprocta apache Davis 1,2

Cixiidae

Oecclus productus Metcalf 1

Cixiid spp. I-II 1

Delphacidae

Delphacodes sp. 1

Delphacid sp. 1

Psyllidae

Psylla sp. 1,2

Trioza maura Foerster 1,2

<u>Craspedolepta minutissima</u> (Crawford)	1
Psyllid spp. I-IV	1
HEMIPTERA	
Berytidae	1
Berytid sp.	1
Coreidae	
<u>Leptoglossus</u> sp.	1
Coreid sp.	1
Lygaeidae	
<u>Geocoris pallens</u> Stal	1
<u>Nysius raphanus</u> Howard	1
<u>Nysius?</u> sp.	1
Lygaeid spp. I-IV	1
Miridae	
<u>Orthotylus</u> sp.	1,2
near <u>Psallus</u> sp.	1,2
<u>Phytocoris</u> sp.	1,2
<u>Parthenicus</u> near <u>ruber</u> Van Duzee	1,2
<u>Parthenicus</u> sp.	1,2
Mirid spp. I-IV	1
Pentatomid	
Pentatomid spp. I-II	1
Pyrrhocorid	
Pyrrhocorid sp.	1
Tingidae	
Tingid sp.	1,2
COLEOPTERA	
Anthicidae	
Anthicid sp.	2
Chrysomelidae	
<u>Diachus ayratus</u> (Fab.)	1,2
<u>Disonycha alternata</u> (Illiger)	2
<u>Glyptina cerina</u> LeConte	2
<u>Pachybrachis signatus</u> Bowditch	1
<u>Pachybrachis bivittatus</u> (Say)	1
<u>Pachybrachis</u> sp.	1
<u>Paria quadriguttata</u> LeConte	1
<u>Phyllotreta lewisii</u> Crotch	2
Hispine spp. I-II	1
Chrysomelid spp. I-VI	1

Curculionidae	
<u>Sibinia</u> sp.	2
Melyridae	
<u>Amecocerus</u> near <u>annulatus</u> (Casey)	1
Mordellidae	
Mordellidae sp.	2
LEPIDOPTERA	
Gelechiidae	
Gelechiid sp.	1
Geometridae	
<u>Semiothisa</u> near <u>fieldi</u>	1,2
Geometrid spp. I-III	1
Nymphalidae	
<u>Nymphalis</u> <u>antiopa</u> Linnaeus	1
Lepidoptera spp. I-II	1
THYSANOPTERA	
Thripidae	
<u>Frankliniella</u> <u>occidentalis</u> (Pergande)?	1
Thripid spp. I-II	1
DIPTERA	
Cecidiomyidae	
<u>Rhabdophaga</u> sp.	1

REFERENCES

- 1 Stevens, 1985
- 2 This study

APPENDIX 3.2b: PHYTOPHAGOUS INVERTEBRATES COLLECTED FROM
TAMARIX CHINENSIS LOUR. IN THE UNITED STATES

ACARINA

	Tetranychidae	
<u>Tetranychus</u>	<u>bimaculatus</u> Harvey	5,7
<u>Acarina</u> sp.		6

ORTHOPTERA

	Gryllidae	
<u>Gryllid</u> sp.		6
<u>Oecanthus</u>	<u>quadripunctatus</u> Beutenmuller	4
	Locustidae	
<u>Aeolopus</u>	<u>arixonensis</u> Schudder	3
<u>Hesperotettix</u>	<u>viridis</u> (Thomas)	8
<u>Melanoplus</u>	<u>differentialis</u> (Thomas)	3,5,7
<u>Melanoplus</u>	<u>occidentalis</u> (Thomas)	5,7
<u>Schistocerca</u>	<u>lineata</u> Schudder	5,7
<u>Schistocerca</u>	<u>shoshoni</u> Schudder	3,6
<u>Schistocerca</u>	<u>vaga</u> (Schudder)	3
<u>Trepidulus</u>	<u>rosaceus</u> Schudder	7

	Phasmidae	
<u>Diapheromera</u>	<u>arizonensis</u> (Caudell)	3
<u>Diapheromera</u>	<u>covilleae</u> Rhen & Hebard	7

HOMOPTERA

	Aphididae	
<u>Aphis</u>	<u>craccivora</u> Koch	5,7
<u>Aphis</u>	<u>gossypii</u> Glover	5,7
<u>Aphis</u>	<u>medicaginis</u> Koch	3
<u>Macrosiphum</u>	<u>pisi</u> (Harvey)	3
<u>Macrosiphum</u>	<u>solanifolii</u> (Ashm.)	3
<u>Myzus</u>	<u>persicae</u> (Sulzer)	3
<u>Aphidid</u> spp. I-IX		6,8

	Cercopidae	
<u>Clastoptera</u>	<u>ovata</u> Doering	7

	Cicadellidae	
<u>Aceratagallia</u>	<u>sanguinolenta</u> (Provancher)	5,7
<u>Aceratagallia</u>	<u>uhleri</u> (Van Duzee)	5,7
<u>Aceratagallia</u>	sp.	5,6,7
<u>Amblysellus</u>	<u>grex</u> (Oman)	6
<u>Balclutha</u>	<u>neglecta</u> (DeLong & Davidson)	7
<u>Ballana</u>	sp.	7
<u>Carneocephala</u>	sp.	5,7
<u>Ceratagallia</u>	<u>neodona</u> Oman	5,7
<u>Chlorotettix</u>	<u>viridis</u> Van Duzee	4

<u>Colladonus belli</u> (Uhler)	5,7
<u>Cuerna stiata</u> (Walker)	7
<u>Doleranus lucidus</u> (Baker)	7
<u>Empoasca abrupta</u> DeLong	3
<u>Empoasca</u> sp.	5,6,7
<u>Homolodisca liturata</u> Ball	3
<u>Idiocerus apache</u> Ball & Parker	7
<u>Idiocerus alternatus</u> Fitch	5,7
<u>Idiocerus nervatus</u> Van Duzee	5,7
<u>Idiocerus rufus</u> Gillette & Baker	5,7
<u>Idiocerus snowi</u> Gillette & Baker	5,7
<u>Idiocerus</u> sp. I	6
<u>Keonolla dolobrata</u> (Ball)	7
<u>Keonolla uhleri</u> (Ball)	5,7
<u>Lonatura salsura</u> Ball	5,7
<u>Macropis viridis</u> (Fitch)	7
<u>Macrosteles fascifrons</u> (Stal)	7
<u>Opsius stactogalus</u> Fieber	3,5,6,7
<u>Xerophloea viridis</u> (Fabricius)	5,7
<u>Cicadellid</u> spp. I-V	6

Cicadidae

<u>Diceroprocta apache</u> Davis	1,2,3,6
<u>Diceroprocta cinctifera</u> (Uhler)	5,7
<u>Tibicen inauditus</u> Davis	5,7
<u>Tibicen townsendi</u> (Uhler)	5,7
<u>Okanagana utahensis</u>	8

Cixiidae

<u>Oecclus campestris</u> Ball	7
<u>Oecclus cucullus</u> Kramer	8
<u>Oecclus decens</u> Stal	3,7
<u>Oecclus venosus</u> Van Duzee	5,7
<u>Oliarus sonoitus</u> Ball	5,7
<u>Oliarus</u> sp.	5

Coccidae

<u>Pulvinaria innumerabilis</u> Rathon	5,7
<u>Coccid</u> spp. I-II	6

Delphacidae

<u>Delphacodes</u> sp.	5,7
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Diaspididae

<u>Chionaspis etrusca</u> Leonardi	3,5,6,8
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Flatidae

<u>Mistharnophantia sima</u> Doering & Shepard	5,7
<u>Ormenis saucia</u> Van Duzee	5,7
<u>Ormenis yumana</u> Ball	3

Membracidae

<u>Cyrtolobus</u> sp.	7
<u>Leioscyta ferruginipennis</u> (Goding)	5,7

<u>Multareis cornutus lawsoni</u> Cook	5,7
<u>Publilia modesta</u> (Uhler)	5,7
Pseudococcidae	
<u>Phenacoccus helianthi</u> (Cockerell)	5,7,8
<u>Puto</u> sp.	7
Psyllidae	
<u>Heteropsylla texana</u> Crawford	5,7
<u>Kuwayama medicaginis</u> Crawford	5,7
<u>Paratrioza cockerelli</u> (Sulc.)	3
<u>Psylla</u> near <u>alba</u> Crawford	5,7
<u>Triozia collaris</u> Crawford	5,7
<u>Psyllid</u> spp. I-II	6
Aleyrodidae	
near <u>Trialeurodes</u>	8
HEMIPTERA	
Berytidae	
<u>Berytid</u> sp.	6
Cydnidae	
<u>Cydnoides albipennis</u> (Say)	7
Coreidae	
<u>Leptoglossus</u> ?	6
<u>Mozena</u> sp.	3
Lygaeidae	
<u>Liorhyssus hyalinus</u> Fabricius	1
<u>Neacoryphus lateralis</u> (Dallas)	7
<u>Nysius raphanus</u> Howard	1,5,6,7
<u>Xyonyssius californicus</u> (Stal)	5,7
<u>Lygaeid</u> spp. I-II	6
Miridae	
<u>Lopidea</u> sp.	7
<u>Lygus hesperus</u> Knight	1,5,7
<u>Lygus lineolaris</u> (P. uB.)	3
<u>Lygus pratensis</u> Linnaeus	4
<u>Melanotrichus coagulatus</u> (Uhler)	5,7
<u>Orthotylus</u> sp.	5,7
<u>Parthenicus</u> near <u>ruber</u> Van Duzee	6,8
<u>Parthenicus</u> sp.II	8
<u>Phytocoris</u> sp.	5,7,8
<u>Polymerus basalis</u> (Reuter)	5,7
<u>Slaterocoris stygicus</u> (Say)	5,7
<u>Mirid</u> spp. I-III	6
Pentatomidae	
<u>Brochymena parva</u> Ruckes	8
<u>Brochymena sulcata</u> Van Duzee	3

<u>Chlorochroa ligata</u> (Say)	3
<u>Chlorochroa sayi</u> Stal	3,7
<u>Pentatomid</u> sp.	6
Pyrrhocoridae	
<u>Euryopthalmus convirus</u> Stal	3
Rhopalidae	
<u>Aufeiuss impressicollis</u> Stal	7
<u>Liorphyssus hyalinus</u> Fabricius	5,7,8
<u>Stictopleurus viridicatus</u> (Uhler)	7
COLEOPTERA	
Anthicidae	
<u>Anthicus cervinus</u> La Ferte	7
<u>Anthicus</u> sp.	5,7
<u>Notoxus caudatus</u> Fall	7
<u>Notoxus calcaratus</u> Horn	7
<u>Anthicid</u> sp. I	8
Bostrichidae	
<u>Amphicerus cornutus</u> (Pallus)	5,7
<u>Amphicerus simplex</u> (Horn)	5,7
Bruchidae	
<u>Acanthoscelides chiricahuae</u> (Fall)	7
<u>Acanthoscelides collusus</u> (Fall)	7
<u>Acanthoscelides compressicornis</u> (Schaeffer)	7
<u>Acanthoscelides fraterculus</u> (Horn)	8
<u>Acanthoscelides prosopoides</u> (Schaeffer)	7
<u>Algarobius prosopis</u> (LeConte)	7
<u>Mimosestes amicus</u> (Horn)	7
<u>Mimosestes protractus</u> (Horn)	7
Buprestidae	
<u>Buprestis confluenta</u> Say	7
<u>Chrysobothris strofasciata</u> LeConte	3
<u>Hippomelas</u> sp.	6
<u>Psiloptera drummondi</u> Castelnau	5,7
Chrysomelidae	
<u>Altica</u> near <u>torquata</u> LeConte	8
<u>Altica</u> near <u>foliacea</u> LeConte	7
<u>Chaeatocnema ectypa</u> Horn	3
<u>Chaeatocnema</u> sp.	7
<u>Colaspoides</u> sp.	7
<u>Coscinoptera</u> near <u>dominicana</u> Fabricius	5,7
<u>Coscinoptera tricineta</u> (Say)	7
<u>Diachus auratus</u> (Fab.)	8
<u>Pachybrachis arizonensis</u> Bowditch	5,7
<u>Pachybrachis croftus</u> Bowditch	7
<u>Pachybrachis hepaticus</u> Melsheimer	4
<u>Pachybrachis</u> near <u>m-nigurm</u> Melsheimer	7

<u>Pachybrachis mitis</u> Fall	7
<u>Pachybrachis sexnotata</u> Bowditch	4
<u>Pachybrachis signatus</u> Bowditch	5,7
<u>Pachybrachis</u> sp.	6
<u>Phyllotreta</u> sp.	7
<u>Trirhabda canadensis</u> (Kirby)	7
<u>Chrysomelid</u> spp. I-VIII	6,8

Cleridae

<u>Cymatodera oblita</u> Horn	7
<u>Enoclerus coccineus</u> (Schenckling)	7
<u>Enoclerus cordifer</u> (LeConte)	7
<u>Enoclerus quadrisignatus</u> (Say)	7
<u>Monophylla californica</u> (Fall)	7
<u>Phyllobaenus</u> sp. I	5,7
<u>Phyllobaenus</u> sp. II and III	7
<u>Trichodes bibalteatus</u> LeConte	7
near <u>Trichodes</u>	7

Cryptophagidae

<u>Cryptophagus</u> prob. <u>croceus</u> Zimmerman	8
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Cucujidae

<u>Ahasverus</u> near <u>advena</u> (Waltl.)	5,7
<u>Oryzaephilus surinamensis</u> (Linnaeus)	5,7

Curculionidae

<u>Apion</u> sp.	5
<u>Epimechus</u> sp.	8
<u>Hypera punctata</u> (Fabricius)	7
<u>Ophryastes</u> sp.	7
<u>Pandeletheinus</u> sp.	7
<u>Sitona hispidula</u> (Fabricius)	7
<u>Smicronyx</u> near <u>interruptus</u> Blatchley	7
<u>Smicronyx</u> near <u>lutulentus</u> Dietz	7

Dermestidae

<u>Cryptohopalum festum</u> Casey	7
<u>Cryptohopalum fontinal</u> Casey	7
<u>Trogoderma stenale</u> Jayne	7

Elaterridae

<u>Dicrepidius corvinus</u> Candeze	7
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Histeridae

<u>Hololepta populnea</u> LeConte	7
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Lyctidae

<u>Trogoxylon aequale</u> (Wollaston)	5,7
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Melyridae

<u>Amecocerus</u> near <u>annulatus</u> Casey	6
<u>Attalus</u> spp. I-III	7
<u>Hypebaeus</u> sp. I	8

<u>Trichochrous</u> sp.	7
<u>Vecturoides pseudonychus</u> Fall	8
Mordellidae	
<u>Diclidia</u> sp. I and II	7
<u>Mordella brevistylis</u> Liljeblad	7
<u>Mordellistena</u> sp.	7
<u>Pentaria trifasciata</u> (Melsheimer)	7
Phalacridae	
<u>Phalacrus</u> sp.	7
Rhipiceridae	
<u>Sandalus californicus</u> Lac.	3
Tenebrionidae	
<u>Tribolium castaneum</u> (Herbst)	7
Scarabaeidae	
<u>Ochsosidia arizonica</u> Casey	3
CORRODENTIA	
Undetermined	3
PSOCOPTERA	
Lachisillidae	
<u>Lachesilla</u> sp.	5,7
<u>Psocoptera</u> sp.	6
LEPIDOPTERA	
Arctiidae	
<u>Estigmene acraea</u> Drury	3
Geometridae	
<u>Geometrid</u> sp.	6
Lyonetiidae	
<u>Bucculatrix</u> sp.	7
Noctuidae	
<u>Tarachidia</u> sp.	7
Psychidae	
<u>Oiketicus townsendi</u> Cockerell	7
<u>Thyridopteryx ephemeraeformis</u> Haworth	4
Pyrilidae	
<u>Crambus</u> sp.	7
Scythridae	
<u>Scythris</u> sp.	7

THYSANOPTERA

	Thripidae	
<u>Franklinella</u>	<u>occidentalis</u>	(Pergande)
Thripid sp.		3,5,6,7 6

HYMENOPTERA (Parasitic)

	Dryinidae	
<u>Gonatopus</u>	sp.	5,6?,7

	Mymaridae	
<u>Barypolynema</u>	<u>saga</u>	Girault
		5,6?,7

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7. Watts et al. (1976)
8. This study